JOURNAL OF AGRICULTURAL RESEARCH

VOL. 61 WASHINGTON, D. C., OCTOBER 15, 1940 No. 8.

ESTIMATES OF PRODUCING ABILITY IN DAIRY CATTLE[1]

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INTRODUCTION

Progress in improving dairy cattle through selective breeding based on production performance is basically determined by the accuracy with which production records indicate inherited differences in producing ability. This accuracy becomes greater with any reduction in the variation caused by nonhereditary influences. Recent expansion in the use of production records for dairy cattle improvement, and the present variety in the kinds of production records and adjustments for developmental or management influences used, indicate the desirability of knowing whether any one kind of record has advantages over the others and which adjustments for nonhereditary influences on production records contribute materially to their accuracy. While numerous investigators have studied the environmental and developmental influences on production and have derived factors for standardizing records for such influences, only limited attention has been given to the relative genetic worth of corrected and raw records, and of the different kinds of production records. In this study the degree of inherency of five kinds of production records, before and after each correction for nonhereditary influences, is determined among the records of the same cows to see which estimate of producing ability is of greatest practical usefulness for selection purposes.

SOURCE OF DATA

The data include 1,574 lactation and 1,456 testing-year records of 274 Holsteins from 41 herds. Special fieldmen obtained the desired records directly from Dairy Herd Improvement Association herdbooks at the farms in connection with herd studies sponsored by the Germ Plasm Survey of the United States Department of Agriculture in 1935. The cows selected for this study were tested during at least their first five lactations and had no recorded mastitis, injury, or abortion, during this time. Testing-year records were discarded for years in which a cow freshened for the first time later than the third month or left the herd before the tenth month. Actual yields were used except

[1] Received for publication January 8, 1940. Paper from the Department of Genetics (No. 255), Wisconsin Agricultural Experiment Station. Some assistance was provided by the National Youth Administration and the Work Projects Administration during the course of the investigation.

[2] The writer wishes to express his appreciation to Dr. L. J. Cole at whose suggestion the work was initiated, and to Drs. A. B. Chapman and L. E. Casida, of the Wisconsin Station, and Dr. J. L. Lush, of the Iowa Station, for many helpful suggestions and for criticism of the manuscript.

for some three and four milkings-per-day records in a few Holstein herds, and these were corrected to a two-daily-milkings basis with Norton's factors (*23*).[3]

METHOD OF INVESTIGATION

Each cow's lifetime production was calculated in terms of five kinds of records (240-day, 305-day, 365-day, total lactation, and testing-year), making it possible to compare the different kinds of records within the same cows and under the same environmental conditions. The means and standard errors for the five kinds of production records and the factors affecting yield are as follows:

Record or factor		*Mean*
First 240-day butterfat yield	pounds	318±1.8
First 305-day butterfat yield	do	362±2.2
First 365-day butterfat yield	do	380±2.4
Total lactation period butterfat yield	do	389±2.7
Calving interval [1]	days	390±1.9
Lactation period length	do	340±1.8
Dry period length [1]	weeks	6.9±0.13
Testing-year butterfat yield	pounds	375±2.3
Period milked during the testing year	days	322±0.8

[1] In some cases the calving interval and following dry period were unknown for the last lactation. Therefore, these means were based on only 1,447 records instead of 1,574.

The measure of usefulness of production records in selecting breeding stock which was employed to determine the value of adjustment for environmental influences, and to compare the five kinds of records before and after such adjustments, was the average within-herd correlation between records of the same cow. This may be termed "repeatability," since it indicates the degree to which records of the same cow repeat themselves (i. e., tend to be more like each other than they are like records of other cows in the same herd). This measure had previously been used by Lush and his coworkers (*20, 21*). It is calculated by the analysis of variance method of Fisher (*8*), in which the ratio of the between-class to the total variance may be expressed either as the portion of the variance due to differences between the classes (e. g., those due to herd differences, or to cow differences within herds), or as the average correlation between observations in the same class (e. g., between records in the same herd, or records of the same cow).

Smaller differences in repeatability are statistically significant when the two variables compared are highly correlated with each other, as in the present study (e. g., the actual and age-corrected records, or the 305-day and 365-day records, for the same lactations), than when two more or less independent variables are compared (e. g., 305-day records in two different breeds, or comparing production in cattle with litter size in swine).

The relative importance of the various sources of environmental variation in production, and the degree of repeatability or inherency of each influence were determined by the analysis of variance method. Whenever the association of environmental influences with each other or with production was essentially linear, the average correlation and regression among records of the same cow were obtained by the analysis of covariance (*8*) and used in calculating the percentage correction factors.

[3] Italic numbers in parentheses refer to Literature Cited, p. 585.

REPEATABILITY OF UNADJUSTED RECORDS

The repeatability of the production records was calculated on a within-herd basis, since the herd differences, which accounted for one-fifth to one-tenth of the total variation in production records (table 1), are greatly influenced by herd differences in management practices while variation between the lifetime averages of different cows in the same herd are more largely genetic in origin. The repeatability of the unadjusted records was obtained primarily for later use in deciding what had been gained by adjustment for nonhereditary influences, and varied from 0.23 for the 240-day to 0.26 for the total lactation records (table 1).

Differences between herds, and between cows in the same herd, accounted for significant[4] portions of the variation in calving interval, lactation length, days milked during the testing year, and dry period length (table 1). Inherent differences between cows in the same herd were most important in dry period length, which is associated with the persistency level of the cow more closely than are lactation length and days milked.

ADJUSTMENT FOR AGE

The data for age are unique in that every cow was on test from her first calving until past the age of maturity. Thus there was no possibility that the mature age records represented a selected group of cows, inherently higher in producing ability than those with immature records, as was the case with the data from which many of the 40 or more sets of age-correction factors have been derived by various workers. There is the possibility, however, that the influence of age in these data may not be entirely representative, if cows staying in the herd for five or more records tend to be those with relatively higher immature records, and if the percentage age change in yield varies with the level of inherent producing ability, as seems likely from these data (*7*) and from the work of Sanders (*28, 30*) and Schmidt (*32*). The average annual production of these cows was 375 pounds of fat, which was significantly greater (by 15 pounds of fat) than that of other cows in the same herds, and probably over 60 pounds above the average of all cows in tested herds.

Sanders (*28, 30*), Schmidt (*32*), Gaines and Palfrey (*14*), Kendrick,[5] Plum (*24*), and others have recognized the complicating effects of selection in their studies of age and have attempted to avoid these difficulties by studying the influence of age within individual animals. Tuff (*34*) and Ward and Campbell (*36*) have proposed a regression equation method of adjustment for age which also corrects for unknown temporary environmental influences on immature records, but allowance for this environmental regression toward the population average can best be made as suggested by Lush (*19*) in a separate calculation which takes into account the number of records for each cow and the individual herd average, and which treats immature and mature records alike.

[4] "Significant" is used throughout to designate differences which would occur by chance alone less than 1 percent of the time; those with a probability of chance occurrence of 1 to 5 percent are termed "barely significant."

[5] KENDRICK, J. F., comp. TESTER'S COMPUTER. U. S. Bur. Dairy Indus., 22 pp. November 1937. [Mimeographed.] See pp. 17–19.

TABLE 1.—*Analysis of variance in actual* [1] *yield and in factors influencing yield due to herd and cow differences* [2]

Source of variation	Variance symbols [3]	Degrees of freedom [4]	Variance in butterfat yield during lactation				Variance in length of lactation period	Degrees of freedom [4]	Variance in—		Degrees of freedom	Variance in testing year	
			First 240 days	First 305 days	First 365 days	Total lactation period			Calving interval	Dry period		Period milked	Butterfat yield
			Pounds	*Pounds*	*Pounds*	*Pounds*	*Days*		*Days*	*Weeks*		*Days*	*Pounds*
Herds	H	(40)	736	1,180	1,266	1,058	255	(40)	388	2.53	(40)	103.6	1,500
Cows within herds	C	(233)	1,068	1,426	2,006	2,676	578	(233)	364	3.75	(233)	86.6	1,533
Records of same cow	R	1,300	3,612	4,820	5,735	7,513	4,077	1,173	4,718	17.90	1,182	926.4	4,886
Correlation between records in same herd.	$\frac{H}{H+C+R}$	----------	.136	.159	.141	.094	.052	----------	.071	.105	----------	.093	.189
Intraherd correlation between records of same cow.	$\frac{C}{C+R}$	----------	[5].228	[5].228	[5].259	[5].263	.124	----------	.072	.173	----------	.085	[5].239

[1] Except for some records corrected for number of daily milkings.

[2] In this and following tables all values are significant ($P<0.01$) unless otherwise indicated; * indicates barely significant values ($P>0.01<0.05$); ** indicates nonsignificant values ($P>0.05$).

[3] Total mean square $=R+\frac{n_c-1}{N-1}\cdot\frac{N}{n_s}\cdot C+\frac{n_h-1}{N-1}\cdot\frac{N}{n_h}\cdot H=\left[\Sigma x^2-\frac{(\Sigma x)^2}{N}\right]\cdot\frac{1}{N-1}$

Mean square between records of same cow $=R=\left[\Sigma x^2-\Sigma\frac{(\Sigma x)^2_s}{n_s}\right]\cdot\frac{1}{N-n_c}$

Mean square between cow means within herds $=R+\frac{N}{n_c}\cdot C=\left[\Sigma\frac{(\Sigma x)^2_s}{n_c}-\Sigma\frac{(\Sigma x)^2_h}{n_h}\right]\cdot\frac{1}{n_c-n_h}$

Mean square between herd means $=R+\frac{N}{n_c}\cdot C+\frac{N}{n_h}\cdot H=\left[\Sigma\frac{(\Sigma x)^2_h}{n_h}-\frac{(\Sigma x)^2}{N}\right]\cdot\frac{1}{n_h-1}$

Where: N=total number of records, n_c=number of cows, n_h=number of herds,
R=variance of records of the same cow,
C=variance of means of cows in the same herd, and
H=variance of herd means.

[4] The degrees of freedom between herds and between cows in the same herd are enclosed in parentheses to indicate that the variances (H and C) are not simply "mean squares" calculated by dividing the "sums of squares" by the appropriate degrees of freedom as is the case with R, the variance between records of the same cow.

[5] C is underestimated for raw production records, since a part of the variance between records of the same cow (i. e., that due to the age increase in yield) is represented only slightly in the variation between the means of different cows. A better estimate of C may be obtained by letting R=variance of the age-corrected record in C=(mean square between cows within herds$-R$)$\cdot\frac{n_c}{N}$. This gives repeatability values of 0.254, 0.252, 0.274, 0.270, and 0.258 for the 240-day, 305-day, 365-day, total lactation, and testing-year records, respectively.

BASIS OF CORRECTION FOR AGE

Age at calving accounted for about one-fifth (0.21) of the total variation in 240-day, but for progressively less of the variation in 305-day (0.17), 365-day (0.13), and total lactation production (0.10), owing to the much greater total variability of the longer records and to a slightly smaller variation between age classes (class intervals of 3 months) for the 365-day and total lactation.[6] Age at the beginning of the year accounted for only about one-twelfth (0.09) of the variation in testing-year yield, even though the total variation was about the same as for 305-day lactation yield (table 1). Plotting production on age (fig. 1) showed that the relationship was essentially linear up to about 5 years of age, and that no average increase in production occurred beyond that point. The only noticeable deviation from linearity was for the few first lactations (8 of a total of 274) of cows calving at less than 21 months of age.

Table 2 shows that the 240-day, 305-day, and 365-day lactation records starting under 5 years of age were significantly correlated with age only among records of the same cow (with the exception of the 240-day record between cows). The fact that persistency declines with age has been shown by Sanders (*25*, *30*), Turner (*35*), Gaines and Davidson (*13*), Gaines (*10*), Fohrman (*9*), and Schmidt (*32*). Sanders' conclusion (*30*) that the greatest age increase in production occurs within a few months after freshening is borne out here by the fact that no age increase in yield occurred beyond the eighth month of lactation (i. e., table 2 shows that the regression of 240-day lactation production on age was about the same as for 305-day and greater than for 365-day records).

Percentage correction factors for 240-day and 305-day lactation records were calculated from their respective linear regressions on age (up to 5 years) among records of the same cow, taking the mean 55-month yield as the mature level.[7] The regression of 305-day yield on age was fitted to the means of 365-day and total lactation yields (for ages under 60 months) in order to obtain the basis for calculating their age-correction factors. The 305-day regression was used for the longer records to exclude the influence of the significantly longer calving intervals and lactations (fig. 1) of first calvers from the age correction, since separate adjustment for variation in these influences was also to be studied.

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[6] For detailed analysis of variance tables, and for other tables pertaining to the data discussed in this paper, reference is made to the following: DICKERSON, G. E. EVALUATION OF SEVERAL ESTIMATES OF INHERENT PRODUCING ABILITY IN DAIRY CATTLE. Unpublished manuscript on file in the Univ. of Wis. library. The analysis of variance tables are summarized in table 9 of the present paper.

[7] For example, the 240-day fat yield values for each age, from which to calculate the percentage age correction factors, were obtained from the regression equation

$$Y=\bar{y}+(x-\bar{x})b$$

where

$\bar{y}$ = mean 240-day yield for ages under 60 months,
$\bar{x}$ = mean age at calving for ages under 60 months,
b = average increase in yield per month increase in age up to 60 months, among records of the same cow.

For 55 months, $Y=296.99+(55-40.26)3.23=344.6$
For 24 months, $Y=296.99+(24-40.26)3.23=244.5$
Correction factor for 240-day records of 24-month-old cows $=\frac{344.6}{244.5}=1.41$

TABLE 2.—*Analysis of covariance between age* [1] *and butterfat yield during lactation*

Source of variation	Degrees of freedom	First 240 days		First 305 days		First 365 days	
		r	*b*	*r*	*b*	*r*	*b*
			Pounds		*Pounds*		*Pounds*
Herd means	40	−0.036**	−0.641**	0.010**	0.217**	0.027**	0.626**
Cow means within herds	233	.196	2.489	.161*	2.656*	.117**	2.171**
Records of same cow	541	.667	3.230	.639	3.251	.562	3.053
Total	814	.506	3.103	.450	3.150	.389	2.952

[1] For lactations starting before 60 months of age. See also footnote 2, table 1.

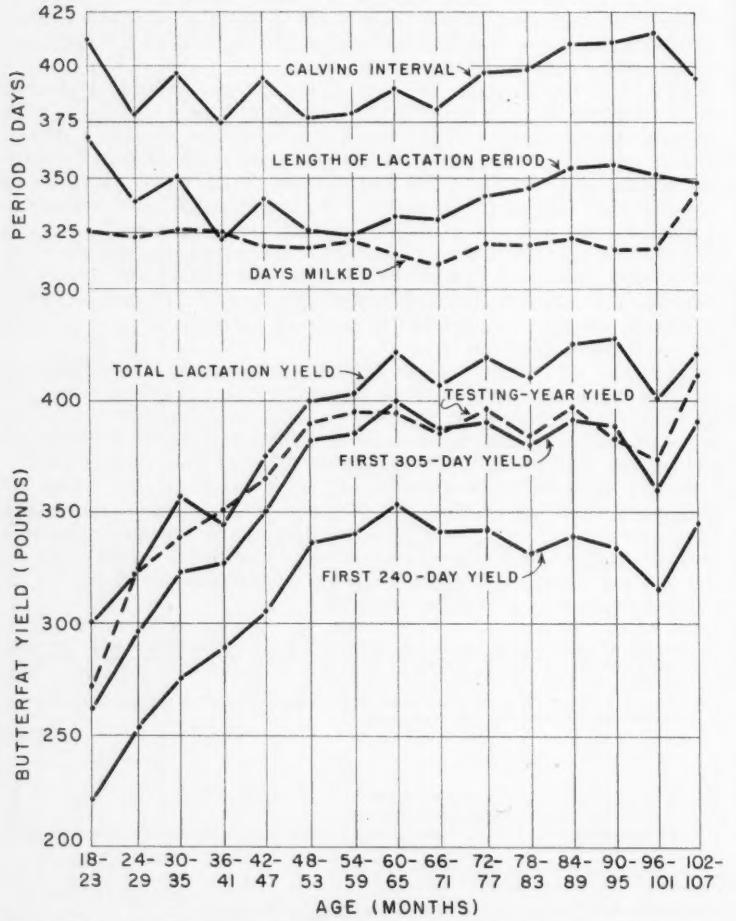

FIGURE 1.—Association of age with calving interval, length of lactation period, length of dry period, and butterfat production.

Factors for age correction of testing-year records were based on the mean testing-year yield and the regression of 305-day yield on age; their only important deviation for the 305-day regression was for the first year records which are lower relative to the first lactation records because the first interval between calvings was longer than later ones. Maximum testing-year production is reached earlier in terms of age at beginning of the testing-year than is maximum lactation yield in terms of age at calving. The age increase in yield occurs chiefly in the early part of the lactation period, and is therefore reflected in testing-year records beginning several months before the start of the lactation period in which the increase actually occurs.

RESULTS OF CORRECTION FOR AGE

Comparison of tables 1 and 3 shows that age correction increased the repeatability of all five kinds of records significantly (by one-sixth to one-half). The increase was greater for 240-day and 305-day than for the longer lactation records and the testing-year record. The increase was accomplished by a sharp reduction in the variation among records of the same cow, accompanied by an increase of similar proportions in the variation between cow means. The increased variation between cow means arose from the use of percentage correction factors greater than unity which add more to the average yield of high than to that of low producers. It has already been shown (7) that the increase in production with age is at least proportional to the producing ability of the cow and that, if anything, high producers are undercorrected and low producers overcorrected by percentage factors. The increase in repeatability of 365-day and total lactation records would have been somewhat greater had the age corrections applied been based on their own respective age changes instead of on the larger regression of the 305-day record on age, since the within-cow variation due to the age decline in calving interval and lactation length (fig. 1) would have been largely removed.

TABLE 3.—*Analysis of variance in age-corrected butterfat yield due to herd and cow differences* [1]

Source of variation	Variance symbols	Degrees of freedom	Variance in butterfat yield during lactation				Degrees of freedom	Variance in testing-year butterfat yield
			First 240 days	First 305 days	First 365 days	Total lactation		
			Pounds	*Pounds*	*Pounds*	*Pounds*		*Pounds*
Herds	H	(40)	815	1, 150	1, 211	1, 164	(40)	1, 517
Cows within herds	C	(233)	1, 369	1, 922	2, 440	3, 036	(233)	1, 991
Records of same cow	R	1, 298	2, 683	3, 663	4, 804	6, 895	1, 182	4, 490
Correlation between records in same herd	$\frac{H}{H+C+R}$		.167	.171	.143	.105		.190
Intraherd correlation between records of same cow	$\frac{C}{C+R}$		.338	.344	.337	.306		.307

[1] See footnotes 2, 3, and 4, table 1.

The smaller increase in repeatability for the testing-year record (change of 0.07 as compared to 0.11 for the 305-day record) was due to the fact that age-correction made only about one-third as great a percentage reduction in the variation among records of the same

cow for the testing-year as for 305-day lactation records, even though both the within- and the between-cow variation in unadjusted records were nearly identical for the two kinds of records. The portion of the variation in testing-year records associated with age at the beginning of the year (0.09) was smaller than that in 305-day records associated with age at calving (0.17). Since the age-increase in production occurs during the early part of the lactation period, it is naturally more closely associated with the age at calving than with the age at the start of a testing association's fiscal year, which bears less relationship to the time of freshening.

ADJUSTMENT OF LACTATION RECORDS FOR ENVIRONMENTAL VARIATION IN LENGTH

The influence of environmental variation in length of record can be minimized either by using a standard length of partial lactation short enough (e. g., 240 days) to avoid the influence of variation in length of time a calf was carried, as suggested by Gaines and Palfrey (*14*), Gowen (*15*), and others, or by adjusting longer kinds of records to a standard length basis as was done by Sanders (*27*, *29*, *30*). Presumably, the latter method would only be desirable if inherent differences in producing ability were more important in the later than in the earlier months of the lactation period. The repeatability in these data of 0.17 for dry period length (table 1) is an indication that important hereditary differences in persistency of lactation do exist, as maintained by Sanders (*25*, *30*), Bonnier (*3*), and others; therefore it seemed worth while to compare the longer kinds of records adjusted to a mature age and standard interval between calving basis with the shorter partial lactation records corrected for age only.

DIRECT CORRECTION FOR CALVING INTERVAL

Variation in length of the interval between calvings was responsible for one-fourth (0.24) of the variation in total lactation records, and for one-tenth (0.11) of that in 365-day records, but for only a small amount (0.05) of the variation in production during the first 305 days of the lactation. Inspection of figure 2 and comparison of the squared gross correlation, 0.214 (table 4), with the between-calving interval classes portion of the variance, 0.236,[8] show that the association of total lactation yield with length of calving interval is essentially linear.

TABLE 4.—*Analysis of covariance of length of dry period and of lactation period, and total butterfat yield, with length of calving interval* [1]

Source of variation	Degrees of freedom	Length of dry period		Length of lactation period		Total butterfat yield during lactation	
		r	*b*	*r*	*b*	*r*	*b*
			Weeks		*Days*		*Pounds*
Between herds	40	0.437	0.0345	0.829	0.761	0.107**	0.184**
Between cows within herds	233	.254	.0191	.799	.787	.517	.906
Between records of same cow	1,173	.400	.0247	.909	.834	.521	.663
Total	1,446	.370	.0246	.878	.817	.463	.661

[1] See footnote 2, table 1.

[8] See footnote 6.

Percentage correction factors[9] were calculated from the average linear regression (0.66 pound per day increase in calving interval,

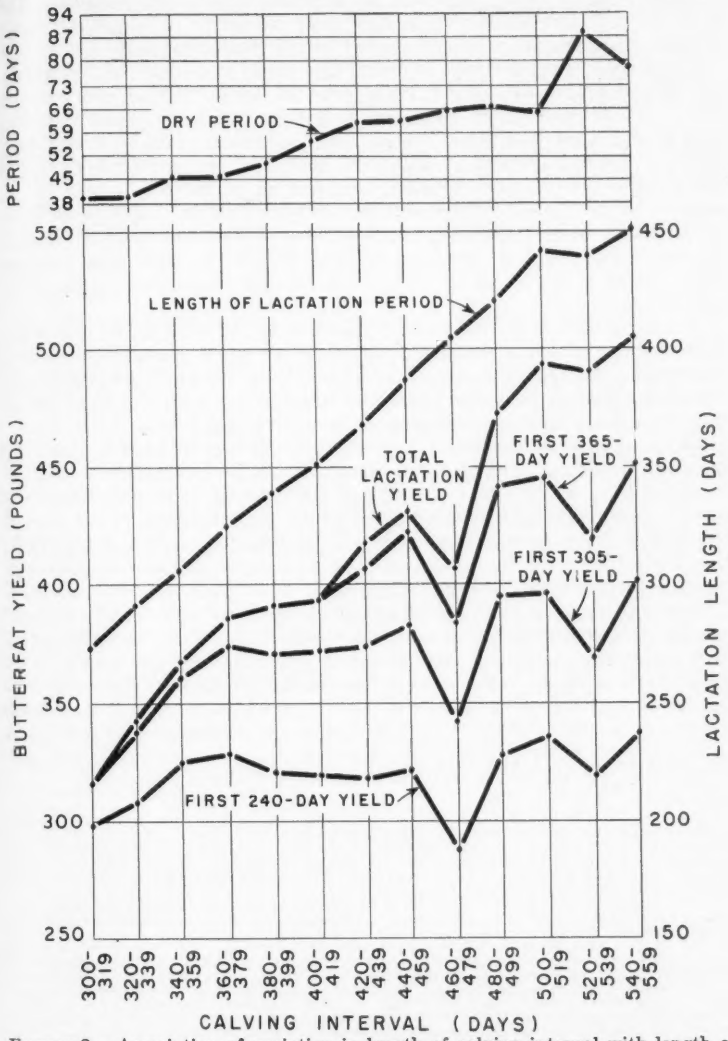

FIGURE 2.—Association of variation in length of calving interval with length of dry period, length of lactation period, and butterfat yield during lactation.

table 4) of total lactation yield on calving interval among records of the same cow. The modal length of 365 days was adopted as the standard length of calving interval to which correction was made. Extremely long intervals caused by breeding troubles accounted for a

[9] See footnote 6.

skewed distribution and a mean length of about 13 months (p. 564) similar to that found by Sanders (*27*), Gaines and Palfrey (*14*), and Schmidt (*32*). Using figure 2 as a guide, the point at which the first 305-day and 365-day lactation yield ceased to be associated with further increases in calving interval length was arbitrarily set at 380 and 460 days, respectively, in correcting these two kinds of "chopped-off" records to a 365-day calving interval basis. When the calving interval was more than 18 months, the first 365-day yield was corrected and used as the estimated total lactation yield in a standard 365-day calving interval. Sanders' (*29, 30*), observation that the percentage factors for adjusting for length of service period (i. e., calving to conception) differed little between first and later lactations, or between persistent and nonpersistent cows, has been found to extend also to different production levels within the same herd in these data; hence a single set of factors for all records should prove fairly satisfactory.

A comparison of tables 3 and 5 shows that adjustment to a 365-day calving interval basis increased significantly the repeatability of age-corrected total lactation records and the between-herd portion of the total variation in both the age-corrected 365-day and the total lactation records; other changes were not significant.[10]

The real gain in heritability resulting from adjustment for calving interval variation was greater than appeared from the increased repeatability, since the influence of permanent cow differences in calving interval length was included in the repeatability of the actual but not of the corrected records.[11] There was probably a net gain in the heritability of the age-corrected 365-day record with calving-interval adjustment for this reason.

It seems clear from the comparison of tables 3 and 5 that adjustment of the age-corrected 365-day and total lactation records for variation in length of the interval between calvings only increases their genetic worth to the same level as that of the 305-day record corrected for age alone. However the results of several other methods of adjusting the age-corrected total lactation yield to a standard length basis will be briefly reported here, lest it appear that the possibilities of the longer kinds of lactation records were not exhausted.

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[10] The percentage reduction in the variation of age-corrected lactation records was considerably greater, particularly among records of the same cow, than the portion of the variation in unadjusted records originally associated with calving interval length (table 4). Correction to a standard (365 days) 1 month below the average in itself would reduce the variation even if all records were reduced by the same percentage. Also the portion of the between-cow variation associated with calving interval had been reduced and that within cows increased by the previous age correction.

[11] The significant repeatability of calving-interval length (0.07, table 1) may be due to intentional or involuntary delayed breeding of better producers, but it is doubtless also associated with the reproductive individuality demonstrated by Chapman and Casida (*6*), which may or may not be associated with productive capacity. In adjusting all records to a 365-day calving-interval basis, the influence of permanent differences between cows in calving-interval length was removed. This was justifiable even if these differences were largely hereditary, for otherwise the variation between cows in calving-interval length would tend to favor the lactation records of inherently "slow breeding" cows and penalize the more regular breeders, ignoring the fact that the goal of selection is efficient reproduction as well as production. The significant difference between the regression of 0.906 between cow means and that of 0.663 within cows in table 4 is evidence that the cows with the longer average calving intervals were higher producers for other reasons. These cow differences associated with calving-interval variation are not removed by adjustment with factors based on the within-cow regression (i.e., $\frac{(0.906-0.663)^2}{(0.906)^2}=0.07$ not removed). Had each cow been adjusted to her own most probable "inherent" calving interval length as calculated by Lush's formula (*19*) (0.31 as much above or below the average for all cows as her own mean length for 6 records indicates), about 24 percent of the between-cow variance associated with calving interval would have remained

$$\text{(i.e., } \frac{[0.906-0.663+(0.31\times 0.663)]^2}{(0.906)^2}=0.24\text{)}$$

instead of only 7 percent.

TABLE 5.—*Analysis of variance in age- and calving-interval-adjusted lactation records due to herd and cow differences* [1]

Source of variation	Variance symbols	Degrees of freedom	Variance in butterfat yield during lactation			
			First 305 days	First 365 days	Total lactation period	Per calving interval day
			Pounds	*Pounds*	*Pounds*	*Pounds*
Herds	H	(40)	1,218	1,312	1,367	0.01201
Cows within herds	C	(233)	1,835	2,079	2,116	.01429
Records of same cow	R	1,298	3,626	3,940	4,004	.03225
Correlation between records in same herd	$\frac{H}{H+C+R}$		.182	.179	.183	.205
Intraherd correlation between records of same cow	$\frac{C}{C+R}$		.336	.345	.346	.307

[1] See footnotes 2, 3, and 4, table 1.

OTHER METHODS OF CORRECTION FOR CALVING INTERVAL

The age-corrected average yield per calving-interval day [12] was considered because of its close association with actual producing efficiency. However, its repeatability (table 5) was no greater than for the age-corrected total lactation record, since dividing by the calving interval greatly overcorrects for the influence of calving-interval variation among records of the same cow,[13] as is also indicated by the results of Chapman and Casida (*5*).

A method of adjusting the age-corrected total lactation record indirectly for calving-interval variation from the length of the lactation period was also tried. Direct adjustment of the age-corrected total lactation record to a standard lactation length with factors based on its average regression on lactation length among records of the same cow would not increase its repeatability because of the important inherent differences between cows in lactation length which are indicated by its repeatability of 0.12 (table 1) and its higher correlation with production between cow means (0.688) than among records of the same cow (0.594) as shown in table 6.[14]

[12] The average dry period for all previous records was added to the lactation length of last lactations for which the calving interval was unknown.

[13] The fact that variation in calving interval length was more highly correlated with the within-cow than with the between-cow variation in yield after correction for age means that the within-cow portion would have been reduced proportionally more by dividing by calving-interval length had the within- and between-cow regressions been the same (table 4). Since the between-cow regression was nearly as large as the mean age-corrected daily yield, while the within-cow regression was significantly smaller, dividing by the calving interval overcorrects for the within-cow influence of calving-interval variation but just removes cow differences in yield associated with calving interval (including the part represented by the difference between the within- and between-cow regressions, which is at least partly due to the better cows being bred later after calving).

[14] Correction factors based on the within-cow regression would remove not only the environmental part of the cow differences in production associated with lactation length (about two-thirds), but also the part due to permanent cow differences in lactation length (about another one-fourth), which are largely due to inherent differences in dry period length but also partly to individuality in calving-interval length. This would leave only about one-tenth, which is not the result of lactation length variation (i.e., represented by the between-cow regression being significantly greater than that within cows). That is,

$$\frac{([0.44\times0.81]+[0.56\times0.81]+[1.21-0.81])^2}{[1.21]^2}=1=$$

between-cow variance correlated with lactation length, when a cow's most probable inherent lactation length is 0.44 as much above or below the mean of all cows as her own average indicates (i. e.,

$$\frac{0.12\times5.75}{1-0.12+(0.12\times5.75)}=0.44,$$

where the intraherd correlation between lactation lengths of the same cow is 0.12 and the average number of records per cow is 5.75). Such adjustment of the age-corrected lactation yield should actually reduce the between- and within-cow variances in nearly the same proportions, since the age-correction decreased the proportion of the between-cow (from 43 to about 38 percent) and increased the proportion of the within-cow variance (from 35 to about 38 percent) which is associated with lactation length (tables 1, 3, and 6).

TABLE 6.—*Analysis of covariance of length of dry period* [1] *and total butterfat yield during lactation period with length of lactation period*

Source of variation	Degrees of freedom	Length of dry period		Degrees of freedom	Total butterfat yield during lactation	
		r	*b*		*r*	*b*
			Days			*Pounds*
Herd means	40	−0.150**	−1.738**	40	0.350*	0.673*
Cow means within herds	233	−.266	−3.472	233	.688	1.211
Records of same cow	1,173	−.034**	−.504**	1,300	.594	.807
Total	1,446	−0.102	−1.432	1,574	0.585	0.885

[1] The regression of lactation length (days) on length of the following dry period (weeks) is given. See also footnote 2, table 1.

Inspection of figure 3 shows that variation in the length of lactations shorter than about 10 months was due largely to cow differences in dry period length, inasmuch as the length of calving interval remained nearly constant, and table 6 shows that dry period was only correlated with lactation length between the means of different cows. The method of correction for lactation length largely avoided removing the cow differences in lactation length under 10 months, since each record was corrected for the average calving interval length for the particular lactation length class with the same factors [15] used in correcting directly for calving interval variation.[16] Comparison of tables 7 and 5 with table 3 shows that this indirect method of calving interval adjustment reduced all portions of the variance in age-corrected total lactation records more than did direct adjustment for calving interval itself, because of the closer association of yield with lactation length (table 6) than with calving interval (table 4). However, the additional reduction was in the same proportion for all portions of the variance, leaving the repeatability and herd portions of the variance the same as for the direct method.

TABLE 7.—*Analysis of variance due to herd and cow differences for age- and lactation length-corrected total lactation records, age-corrected average daily yield between dry dates, and for testing-year records corrected for age and days milked* [1]

Source of variance	Variance symbols	Variance in butterfat yield during lactation			Variance in testing year	
		Degrees of freedom	Total lactation period	Average daily between dry dates [2]	Degrees of freedom	Butterfat yield
			Pounds	*Pounds*		*Pounds*
Herds	H		1,279	0.01153	(40)	1,339
Cows within herds	C	(40)	1,983	.01526	(233)	1,701
Records of same cow	R	(233)	3,656	.02610	1,182	3,941
	H	1,298				
Correlation between records in same herd	$\frac{H+C+R}{C}$		.173	.218		.192
Intraherd correlation between records of same cow	$\frac{C}{C+R}$		.352	.369		.301

[1] See footnotes 2, 3, and 4, table 1.
[2] Age corrected butterfat yield for total lactation period divided by the number of days in the total lactation period and the dry period preceding it.

[15] See footnote 6.
[16] For example, the average calving interval for lactations shorter than 280 days was 335 days, and the factor for adjusting 335-day calving interval records to a 365-day basis was 1.06.

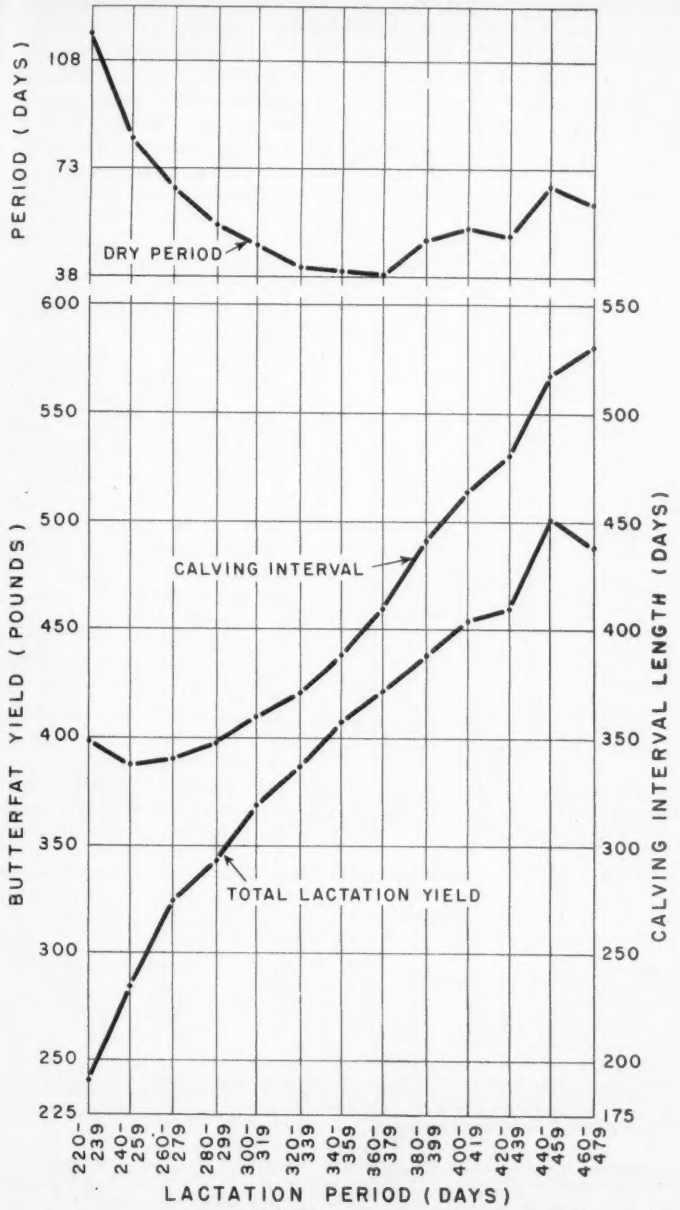

FIGURE 3.—The association of length of lactation period with length of dry period, length of calving interval and total butterfat yield during lactation.

ADJUSTMENT OF TESTING-YEAR RECORDS FOR NUMBER OF DAYS MILKED

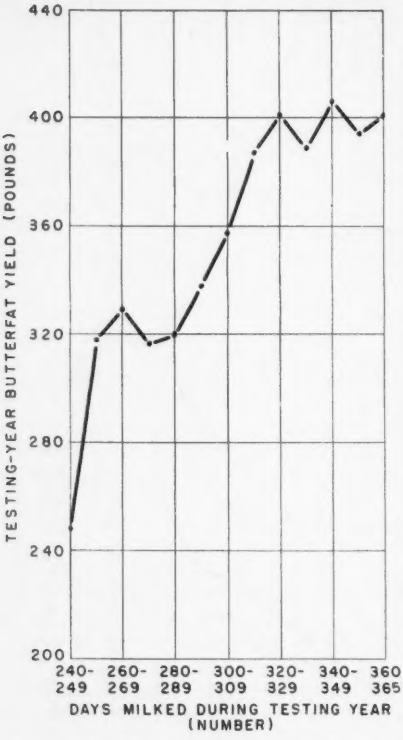

FIGURE 4.—The association of testing-year butterfat yield with the number of days milked during the year.

A comparison of tables 7 and 3 shows that no gain in repeatability is obtained by adjusting the age-corrected testing-year record to a standard 325-days-milked basis with percentage factors [17] based on the regression of production on number of days milked among records of the same cow, even though the association was essentially linear, as shown in figure 4 and by a comparison of the squared gross correlation (0.122, table 8) with the portion of the variance occurring between 10-day classes in days in milk (0.146). The explanation lies in the fact that variation in number of days milked accounted for over twice as much of the variation in testing-year records between cow means as among records of the same cow (table 8), because of the significant repeatability in number of days milked (0.08, table 1) and also because the number of days milked varies greatly in the part of the lactation period it represents in different testing-year records of the same cow.[18]

TABLE 8.—*Analysis of covariance between days milked and testing-year yield* [1]

Source of variation	Degrees of freedom	r	b
			Pounds
Herd means	40	0.461	1.704
Cow means within herds	233	.431	1.440
Records of same cow	1,160	.291	.736
Total	1,433	0.350	1.012

[1] See footnote 2, table 1.

[17] See footnote 6.

[18] Since age-correction decreased the between-cow portion (from 0.18 to about 0.14) and increased the within-cow portion (from 0.08 to about 0.09) of the variance in testing-year records associated with days milked (tables 1, 3, and 8), correction for days milked with factors based on the within-cow regression would presumably reduce the between-cow variance at least as much as that within cows (i. e.,

$$0.14-\frac{(1.44-74)^2}{(1.44)^2}\times 0.14 \geqq 0.09-\frac{(0.74-0.74)^2}{(74)^2}\times 0.09$$

leaving unchanged or slightly reducing the repeatability. Even though it were possible to remove only the temporary environmental differences between cows in days milked, the between-cow variance would be reduced about as much as that within cows. That is, $0.14-\frac{(1.44-0.74+(0.3\times 0.74))^2}{(1.44)^2}\times 0.14=0.083$ when a cows' most probable inherent number of days milked is only 0.3 (i. e., $\frac{0.08\times 5.3}{1-0.08+(0.08\times 5.3)}$) as much above or below the mean for all cows as her own average indicates the number of records per cow being 5.3 and the intraherd correlation between records of the same cow being 0.08 for number of days milked.

OTHER INFLUENCES ON PRODUCTION

Of the remaining factors affecting butterfat production the feeding practice was undoubtedly the major one, influencing herd differences in production more than variation from year to year or from cow to cow in the same herd, as Plum (*24*) has shown. Unfortunately, the information on feeding practices in the present data is unsatisfactory for the study of their influence on production.

LENGTH OF PRECEDING DRY PERIOD

In the present data the influence of variation in length of preceding dry period was similar to that found by Sanders (*29*, *30*), Tuff (*34*), Arnold and Becker (*1*), and others, in that production appeared to increase with length of dry period up to about 1 month and then decline for lactations following dry periods of over 2 months (fig. 5). Actually, the apparently lower production following the longer dry periods indicates that these are records of the inherently nonpersistent, lower producing cows,[19] as also noted by Sanders (*30*).

The rather abrupt increase in yield as dry period is increased up to about 1 month corresponds to that found for persistent producers by Sanders (*30*), and is interpreted to mean that a minimum dry period of about a month is needed in the physiological preparation for maximum daily yield. Increasing the

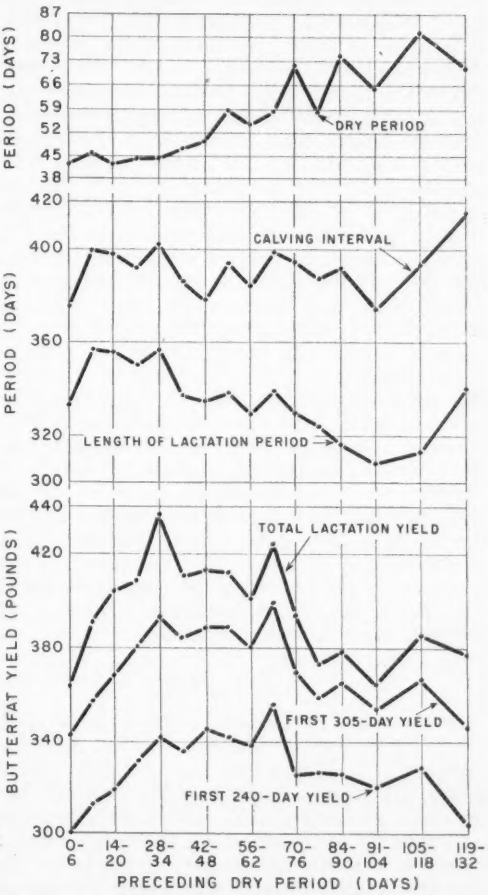

FIGURE 5.—Association of length of preceding dry period with length of calving interval, length of lactation period and butterfat yield during lactation.

[19] The increase in the following dry period length as the preceding dry period increased beyond 1 month (fig. 5) accounted for 0.09 of the following dry period variance, which corresponds to a gross correlation (including herd differences) of about 0.3 between successive dry periods of the same cow. This is only slightly higher than the average gross correlation of 0.26 between any two dry periods of the same cow calculated from table 1. Since successive dry periods should be more alike than those separated by a greater age difference, one concludes that the increase in dry period length with calving interval remaining constant following longer preceding dry periods (fig. 5) was due to inherent cow differences in dry period length or persistency of production, and accounts for the apparent decline in production as the length of preceding dry period increases beyond 2 months.

length of dry period beyond this point probably increases the persistency, as shown by Sanders, but in figure 5 this tendency is obscured by the inherent cow differences in dry period length.

No correction factors for previous dry period variation are presented because: (1) The influence of dry period length on subsequent lactation yield was slight, even though significant (0.03 to 0.04 of the variation in lactation records); (2) the association was greater in the lower than in the higher producing herds (7) and undoubtedly differed for persistent and nonpersistent cows, and for second and later lactations, as shown by Sanders (*29*, *30*); and (3) each cow's records would need to be corrected to her own inherent length of dry period. However, a rough method of correcting the total lactation record simultaneously for variation in both preceding dry period and calving interval length was attempted. The age-corrected total lactation yield was divided by the number of days in the total lactation period and the dry period preceding it.[20] By this method the lactation yield is not overcorrected as much for calving interval variation as was true in calculating the average daily yield for the calving interval, since the longer calving intervals were accompanied by longer following dry periods (table 4, fig. 2), but not by longer preceding dry periods (fig. 5). Furthermore, each cow's records tended to be corrected to her own average dry period length, leaving inherent differences in persistency undiminished.

Comparison of tables 7 and 3 shows that both the repeatability and the between-herd portion of the variation in age-corrected total lactation yield were significantly increased by dividing by the period between dry dates, whereas no increase in repeatability resulted from dividing by the calving interval length (table 5). The variation between cows was about the same as for the average age-corrected yield per calving interval day, for the lifetime average of these two figures for a cow agree almost exactly. However, the variation between records of the same cow was significantly less for the age-corrected daily yield between dry dates than for yield per calving interval day, giving the former the greater value in predicting real differences between cows in producing ability.

SEASON OF CALVING

Of the many investigators who have studied the influence of season of calving on production, Sanders (*26*, *30*), Karl Schmidt (*32*), Fr. H. Schmidt (*31*), Marcq and Devuyst (*22*), Cannon (*4*), Plum (*24*), and others, all seem to agree that the unfavorable months for freshening are those associated with poorer feed conditions, particularly in the early months of the lactation period, and that the time of calving best suited to a particular locality depends on the seasonal variation in kind and quality of feeds available. In the present study season of calving (8 classes of 1½ months each) accounted for 0.036 of the variance in the 240-day yield for Holsteins, and for a progressively smaller proportion of the variance in 305-day and 365-day lactation records (0.019 and 0.010, respectively). The association with total

[20] Since the first lactation has no preceding dry period as such, the approximate modal dry period length (45 days) was added to the first lactation length to make its average daily yield figure more comparable to that of later records.

lactation records was not statistically significant (0.003).[21] Production was lowest for cows calving from April to September and highest for cows calving from October to March (fig. 6), the difference closely resembling that found by Plum and by Cannon in Iowa testing association records.

The smaller relative influence on the longer kinds of lactation records was due to the greater total variance for longer records, and to the barely significant tendency shown in figure 6 and table 9 for cows freshening from April to September to have the longer lactations and calving intervals.

Because of its relative unimportance and the tendency, shown by Sanders (*30*), for the records of persistent cows to be less affected than those of nonpersistent cows, no correction for season of calving was attempted.

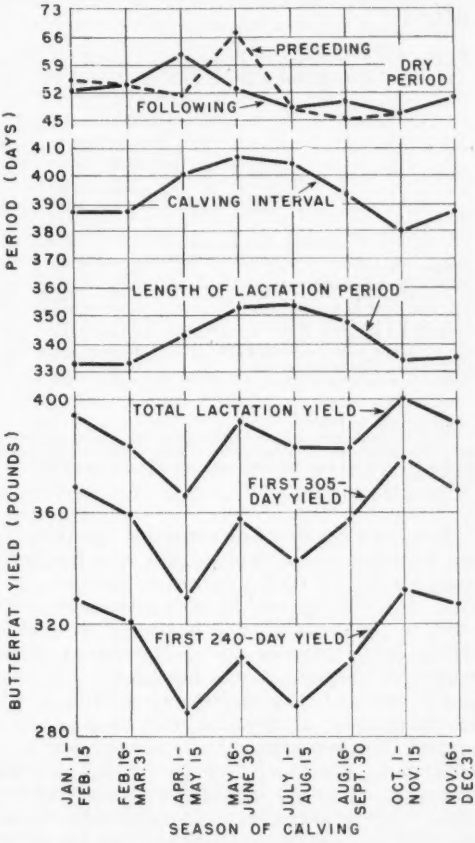

FIGURE 6.—Association of the season of calving with calving interval, length of lactation period, length of preceding and following dry period, and butterfat yield during lactation.

DISCUSSION OF RESULTS

The central objective of this investigation was to determine what kind of modified production record most accurately reflects hereditary differences in producing ability. The data studied did not permit a direct determination of the portion of the variation in production which was hereditary in the narrowest sense (i. e., transmitted from parent to offspring). Therefore, it was necessary to use a closely related criterion, the portion of the variance in yield associated with inherent (i. e., permanent or average lifetime) differences between cows in the same herd environment. As Lush and his coworkers

[21] See footnote 6.

(*20*, *21*) point out, inherent differences between cows include hereditary differences which are transmitted, those which may not be transmitted (such as effects of dominance and epistasis), and permanent differences in environment (i. e., in addition to those which would occur by chance alone).

TABLE 9.—*Percentage of variance in several environmental factors and in different kinds of production records associated with various environmental influences* [1]

Variables affected	Number of records	Percentage of variance for indicated environmental influences					
		Total variance [2]	Age	Preceding dry period	Season of calving	Calving interval length	Lactation length
Calving interval	1,447	5,460	1.5	0.6**	0.7*		
Lactation period length	1,574	4,902	1.4*	2.2	.6*	78.4	
Dry period length	1,447	24.1	1.6	8.9	.7*	18.4	
First 240-day butterfat yield	1,574	5,396	21.2	3.8	3.6	1.1**	3.9
First 305-day butterfat yield	1,574	7,394	16.9	3.9	1.9	4.8	11.9
First 365-day butterfat yield	1,574	8,971	13.4	3.9	1.0	11.1	21.7
Total lactation period butterfat yield	1,574	11,214	10.5	3.3	.3**	23.6	35.7
Days milked, during testing year	1,434	878	1.4				
Testing-year butterfat yield	1,434	7,332	8.7				[3] 14.6

[1] See footnote 2, table 1.

[2] First lactations were necessarily omitted in studying the influence of preceding dry period length, so that the total variances for variables associated with it differed slightly from those given in this table. The same applies to variables associated with calving interval length which was unknown for the last lactations of some cows.

[3] Days milked.

For the purpose of determining the relative genetic worth of different kinds of production records, the fraction of the within-herd variance associated with inherent or permanent differences between cows (i. e., the average within-herd correlation between records of the same cow, or "repeatability") is nearly as useful as the fraction of the within-herd variance due to hereditary differences transmitted from parent to offspring would have been, since these two fractions bear a fairly constant relationship to each other. The quantity included in the numerator of the first fraction but not in the numerator of the second (the dominance and epistatic variations not transmitted, and permanent effects of environment) would be the same for different measures of producing ability, unless some discount the relatively small permanent effects of environment more than others. Lush and Arnold (*20*) have estimated that the second fraction (heritability) comprises about two-thirds of the first (repeatability) for butterfat production records.

An instance of removal of permanent differences between cows occurred when the influence of the 6 percent of within-herd variation in calving interval due to cow differences was removed by correction to a yearly calving basis. The net gain in heritability from such correction therefore was greater than indicated by the increase in repeatability.

It has been shown that the effect of an environmental influence on production among records of the same cow may not be represented truly in the gross association because of (1) the effects of selection on the data (e. g., as in culling with age), (2) hereditary differences in an influence which is also an environmental source of variation among records of the same cow (e. g., as in lactation and dry period length),

and (3) permanent environmental differences between herds or between cows in the same herd (e. g., as in length of calving interval). In the present study these factors have been taken into account and the average association among records of the same cow determined by the covariance technique whenever the association was a linear one.

Adjustment with percentage correction factors assumes that cows of different levels of persistency or of producing ability make about the same proportional (but not absolute) change in production with a given environmental difference. Sanders (*26, 28, 29, 30*) has demonstrated that persistent and nonpersistent cows do not make the same percentage change with age, previous dry period, or season of freshening, as previously discussed, and that the effect of dry period differs for second and later calvers. In the present data, the age increase at different levels of producing ability did not differ significantly from that assumed in using percentage age-correction factors, but the increase in production with longer preceding dry periods was greater rather than less for cows in the lower producing herds, making the use of a single set of factors for dry period length on all records entirely unsatisfactory (*7*). Percentage correction factors for calving interval variation should be fairly satisfactory, however, judging from Sanders' (*27*) (*30*) finding that the percentage change in total lactation yield with service period (calving to conception) differed little for persistent and nonpersistent producers or for first and later lactations, and from the fact that no consistent differences in the percentage factors were found between different production levels of herds or of cows within herds in the present data.

Sanders (*30*) and Gaines (*11*) have studied the increase in repeatability of production records with correction for environmental influences. Sanders found that correction of the total lactation milk yield for season, age, dry period, and service period increased the within-herd correlation between records of the same cow from 0.52 to 0.73. In the present study, correction of the total lactation yield for age and calving interval (no correction for dry period and season) increased the repeatability from 0.26 to 0.35. Sanders' corrections for dry period and season would have increased the between-cow and further reduced the within-cow variance. Overlooking the differences in level of repeatability in the two studies (discussed later), the proportional gain in repeatability with correction for environmental influences is similar in both. The failure of correction for age and number of daily milkings to increase the repeatability of Holstein Herd Improvement Register 365-day lactation records reported by Gaines was probably due to the important cow differences in number of daily milkings in his data removed by such corrections. Cow differences remaining after the corrections would be more largely hereditary than those in the actual records; thus the heritability, or value of the records for selection purposes, was undoubtedly increased by the adjustment for age and daily milkings.

Which of the five kinds of production records best measures inherent differences in producing ability? It is apparent that the repeatability of age-corrected 240-day and 305-day records was just as great as for the 365-day and total lactation yields corrected for both age and length of calving interval (table 10). The age-corrected testing-year record was lower in repeatability than were the age-corrected

240-day, 305-day, and 365-day lactation records, because the association between age at calving and lactation yield was much closer than between age at the beginning of the year and testing-year yield (table 9) for reasons previously discussed (p. 568). The difference which Harris, Lush, and Shultz (*18*) found in favor of the age-corrected 365-day lactation record (0.34 to 0.31) was duplicated in the present study (0.34 to 0.31). Furthermore, the lactation record may be susceptible of further improvement in accuracy by proper correction for length of preceding dry period and for season of calving, while the testing year is not. However, the testing-year record, in common with the average daily yield for the calving interval or for the period between dry dates, does have the possible advantage of reflecting cow differences in regularity of reproduction which the lactation records do not. Thus it appears that the age-corrected 305-day lactation record now in general use is fully as satisfactory for the purposes of selecting for producing ability as any of the other kinds of records. It also becomes available sooner and entails less work in computation than the age- and calving-interval-corrected 365-day or total lactation records.

TABLE 10.—*Summary of relative genetic worth of various estimates of producing ability and of the importance of herd and cow differences in factors influencing yield*

Kind of record	Correction	Variance between records of same cow, R [1]	Correlation between records in same herd, $\frac{H}{H+C+R}$ [1]	Intraherd correlation between records of the same cow, $\frac{C}{C+R}$ [1]
ESTIMATES OF PRODUCING ABILITY				
First 240-day butterfat yield	None [3]	3,612	0.14	[2] 0.23
	Age	2,683	.17	.34
First 305-day butterfat yield	None [3]	4,820	.16	[2] .23
	Age	3,663	.17	.34
	Age, calving interval	3,626	.18	.34
First 365-day butterfat yield	None [3]	5,735	.14	[2] .26
	Age	4,804	.14	.34
	Age, calving interval	3,940	.18	.35
Total lactation period, butterfat yield	None [3]	7,513	.09	[2] .26
	Age	6,895	.10	.31
	Age, calving interval	4,004	.18	.35
	Age, lactation length	3,656	.17	.35
Age-corrected average butterfat yield per calving interval day.		.03225	.20	.31
Age-corrected average butterfat yield per day between dry dates.		.02610	.22	.37
Testing-year, butterfat yield	None [3]	4,886	.19	[2] .24
	Age	4,490	.19	.31
	Age, days milked	3,941	.19	.30
FACTORS AFFECTING PRODUCTION				
Calving interval ..... days		4,718	.07	.07
Dry period length ..... weeks		17.90	.10	.17
Lactation period length ..... days		4,077	.05	.12
Period milked during testing year ... do		926.4	.09	.08

[1] See footnote 3, table 1.
[2] Underestimated by about 0.02. See footnote 5, table 1.
[3] Except for number of milkings per day to a two-time basis.

Since the age-corrected 240-day yield is no less repeatable than the 305-day or 365-day yields in these data, one wonders whether a still shorter partial lactation might not do as well. Gaines (*12*) has shown that the average correlation between two successive actual fat records of the same cow in Guernsey Advanced Register records from many herds increases steadily from 0.51 for the first 2-month partial lactation to 0.68 for 365-day lactation yield. However, even though the first 2-month yield was just as repeatable as the 10-month yield, the latter would be preferable because it is more highly correlated with the goal of selection—high average lifetime production. The first 2-month yield measures only the maximum productive capacity; the 10-month yield measures the degree of persistency as well as maximum producing ability.

Now the question arises, what is the actual repeatability or predictive value of the best estimate of producing ability within the individual breeder's herd? In comparing the estimates of the within-herd repeatability found in various studies the effect of the number of records per cow on the estimate of repeatability must be considered. One would expect the environmental variation between successive records of a cow to be less than between records separated by a number of years during which greater changes in age, management conditions, disease, etc., may influence her production, as shown by Berry and Lush (*2*). Also, Seath's results (*33*) indicate that inherent differences between cows are likely to be smaller in a population of cows from which those culled before completing their fifth lactation have been eliminated than in a population which includes all cows with two or more records. Furthermore, time trends and yearly variations in management conditions are more likely to cause "permanent" environmental differences in production between cows having only 2 records each than among cows having 5 to 10 records each.

In Gowen's (*16*) Holstein Advanced Register data, 0.33 of the variation was due to herd differences. Thus his correlation between two successive records of the same cow would become 0.51 when calculated on a within-herd basis, as in the present study. Assuming the same herd variation, his repeatability figure for Guernsey (*16*) milk yield would become 0.55 and for Jersey (*17*) milk yield between 0.4 and 0.6, both of which are similar to his estimate of 0.54 from a single Jersey herd (*15*).

In studies of Harris, Lush, and Shultz (*18*) and Plum (*24*) all cows with two or more records were used, herds tested for 3 or more years being included. Gowen's various estimates of the within-herd repeatability of 0.5 or thereabouts were higher than Plum's estimate of 0.4 because only successive records of a cow were used, and perhaps also because of greater differences in environment affecting individual cows in Advanced Register testing (in number of daily milkings, especially). Sanders' estimate (*30*) of 0.7 is still higher than Gowen's, because in addition to using only two successive records of a cow he adjusted for variation in dry period and season as well as for age and calving interval differences. The lower repeatability of age- and calving interval-corrected lactation yield in the present study (0.35) is apparently due to the more select group of cows taken from each herd (only those with five or more records) and to smaller permanent

environmental differences between cow means (three and four daily milking records were corrected to a two-milking basis here, while Plum's were not), since the between-cow variance in age-corrected 240-day yield was smaller (1,369) than in Plum's data (1,707), while the within-cow variances were similar (2,683 as compared to 2,554). Gaines and Palfrey's estimate (*14*) (0.5 for cows with 10+ lactations) includes herd differences and would probably be around 0.3 on a within-herd basis, being about as much lower than Plum's as in the present study and for similar reasons. Permanent environmental differences between cows (from year-to-year variation in herd environment) probably account for less of the repeatability in Gaines and Palfrey's and in the present study than in any of the others, including Sanders'. The repeatability of 0.33 obtained by Harris, Lush, and Shultz for age-corrected 365-day lactation fat yield is lower than Plum's estimate of 0.40, probably because Plum used age-correction factors carefully calculated from his own data, while the former used the old 70-, 80-, and 90-percent factors for 2-, 3-, and 4-year-old records. Plum's estimate of 0.4 is the one which is most nearly typical of the average within-herd repeatability of age-corrected 240-day or 305-day lactation records in breeders, herds where all cows are production-tested every year, and some are milked three times daily. Adjustment for frequency of milking would lower this repeatability figure slightly.

No satisfactory method has been devised for determining what part of the differences between herd averages is due to hereditary differences between the cows. Plum (*24*) has shown that herd differences in feeding practice are associated with at least one-third of herd differences in age-corrected 240-day lactation yield, and has estimated that all environmental herd differences probably account for over half of the herd variation in yield, leaving somewhere near two-fifths to be explained by hereditary differences (including effects of dominance and epistasis) between the cows in different herds. Harris, Lush, and Shultz (*18*) are in agreement with Plum in his conclusion that herd differences account for about one-third of the total variation in age-corrected yield. In the present study, only one-fifth to one-sixth of the total variation in age- and length-corrected lactation butterfat yield was accounted for by differences between herd averages (table 10). A comparison of the analysis of variance in age-corrected 240-day lactation yield for Plum's and the present study reveals that the variance between herds is less than half as great in the present study (815 as compared to 2,199), while the variance among records of the same cow is quite similar (2,683 as compared to 2,553) in the two studies.

Two facts account for the smaller differences between herds in this study. (1) Selecting only herds tested for at least 5 consecutive years automatically eliminated many of the lower-producing herds. The average production in the herds used was at least 50 pounds of fat above the mean for all tested herds. This in itself reduced the variation between herd means in these data below that found in the data of Harris, Lush, and Shultz, and Plum, which included herds tested for only 3 years. (2) Records during which a cow was milked three or four times daily were adjusted to a twice-a-day milking basis in this study but not in the other two studies. Since there was considerable uniformity in the number of daily milkings practiced within each

herd, correction to a two-daily-milking basis reduced the herd differences due to management practices. The extent to which the smaller herd variation in this study was more largely hereditary in origin than that found by Harris, Lush, and Shultz, and by Plum, depends on the degree to which environmental differences between herds were minimized more than was hereditary variation by using only herds which had been tested for a long time and by correcting all records to a two-daily-milking basis.

To the skillful breeder, production records are considerably more useful in comparing animals than these studies would indicate, since he knows and can make more accurate allowance for the influence of changes in age, feeding, and other environmental fluctuations than can possibly be incorporated in corrections applied to all herds alike. This means that the careful breeder will make fewer mistakes in his selections of breeding stock within his own herd or in herds with which he has constant contact than in selecting animals from outside herds. As Berry and Lush (*2*) point out, the large amount of unexplained variation between records of the same cow means that the lifetime average production will always be more useful than single records in comparing the inherent producing ability of different cows, and that the herd average and the number of records each cow has should be considered in comparing animals.

SUMMARY

Lifetime butterfat production records of 274 Holsteins from 41 herds were studied to determine what adjustments for environmental influences are advisable and the relative usefulness of five kinds of adjusted records (240-day, 305-day, 365-day total lactation, and testing-year) in selecting for producing ability. The average within-herd correlation between records of the same cow (repeatability) was the criterion used in evaluating adjustments and comparing kinds of records, since it measures the degree of accuracy with which records of different cows indicate real differences in their relative producing ability. Correction factors for influences linearly associated with production were based on the average association among records of the same cow determined by the covariance technique. The analysis of variance was used to determine the relative importance of each environmental influence as a source of variation in production and in other environmental influences (summarized in table 9), and the repeatability and between-herd portion of the variation in the various kinds of actual and adjusted records and factors influencing production (summarized in table 10).

A significant increase in repeatability of all five kinds of records resulted from age-correction with percentage factors based on the essentially linear association of production with ages up to 5 years. The increase was greater for 240-day or 305-day lactation (one-third) than for testing-year records (one-fifth), chiefly because age at the beginning of the testing year was less closely associated with the age change in production (which occurs during the early part of the lactation period) than was age at calving. The increase was smaller for 365-day and total lactation records (one-fifth and one-ninth) because of the greater variation from other sources in the longer kinds of lactation records.

Correction for calving interval to a 365-day basis, with factors based on its linear association with production, increased the repeatability of total lactation (and probably the heritability of 365-day) records significantly, in spite of removing permanent (hereditary and environmental) cow differences in calving interval length. The same increase in repeatability was secured by an indirect method of correcting for calving interval from the lactation length of each record. Dividing the age-corrected total lactation record by the number of days between calvings greatly overcorrected for the influence of calving interval among records of the same cow and did not increase the repeatability; however, dividing by the number of days in the lactation period and preceding dry period tended to adjust each cow's records to her own average preceding dry period length and more satisfactorily corrected for variation in the interval between calvings, increasing the repeatability significantly.

There were important differences between cows in the same herd in inherent dry period length (which reflects persistency), and hence in lactation length and days milked during the testing year, which made adjustment of production records for only the environmental variation in these influences difficult or impractical. The cows with the shorter mean lactation lengths were much lower producers and had much longer dry periods than would have been expected from the average association among records of the same cow. The same was true of the cows milked fewer days during the testing year on the average. Lactation length could be used only indirectly to predict the calving-interval length for which adjustment was made. Adjustment of the age-corrected testing-year record for days milked with factors based on the linear within-cow regression did not change the repeatability. No percentage factors for adjusting for preceding dry period length were used, since its influence varied inversely with the herd production level.

Season of calving was a relatively unimportant source of variation in production and no correction factors are presented. The effects of feeding were not studied. The values found for the between-herd portion of the variance (one-fifth to one-sixth) and the repeatability (one-third) of age and length-corrected records are lower than would be found among records of all cows in production-tested herds because only cows with records for at least their first five lactations from herds with three or more such cows were selected for this study.

The age-corrected 240-day and 305-day lactation records were equal to the age- and calving-interval-corrected 365-day and total lactation records and superior to the age-corrected testing-year record in repeatability; the portion of the variance due to herd differences was identical for these five kinds of records; and the average age-corrected daily yield between dry dates was at least equal to any of these five estimates of producing ability in both respects. The age-corrected 305-day record is probably the most satisfactory for selection purposes, since it becomes available sooner and is easier to compute than any of the other kinds of records except the age-corrected 240-day record. which is less desirable than the 305-day record because it is not as closely correlated with average lifetime production—the ideal measure of performance.

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EARLY RECOGNITION OF THE FREEMARTIN CONDITION IN HEIFERS TWINBORN WITH BULLS[1]

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INTRODUCTION

A freemartin, according to definition by Webster, is a sexually imperfect, usually sterile, female calf, twinborn with a male. Dairy-cattle-breed associations refuse to register a female twinborn with a bull until after she has freshened. The possibility that such individuals will be capable of reproduction is so slight that many breeders destroy them soon after birth. However, breeders of high-producing herds, in which heifer calves are valuable, are often willing to spend the time and expense to raise such individuals to breeding age in the hope that they will prove to be sexually normal.

A number of cases of twin births involving both sexes have occurred in the dairy herd of the Bureau of Dairy Industry at Beltsville, Md. The results of studies of the females of these mixed twins are presented herein to provide additional knowledge about the nature of the abnormalities found in freemartins, with the hope of furnishing criteria that will aid in determining at an early age, whether the female of mixed twins is a freemartin or is normal.

REVIEW OF LITERATURE

The freemartin has been known to cattle breeders since before the establishment of the Roman Empire. The sterile cow born twin with a bull was referred to by Varro, a writer who died in 28 B. C. It was called "taura," which apparently meant "barren cow." Although the condition has been recognized for some 2,000 years the origin of the term "freemartin" is obscure. According to one authority the word "free" meant "willing" or "ready to go," as the freemartin was supposed to be an especially willing worker. It has been proposed also that the word "free" was used to signify exemption from reproduction (sterile). Another authority saw in the term a contraction of the words "ferry," "ferow," or "farrow," which appear to be associated with the Flemish "varvekoe"—a cow that gives no milk—and with the West Flemish "varwekoe"—a cow that has ceased to be capable of producing offspring. It is not difficult to imagine an association between the two words "free" and "farrow."

There is probably greater speculation about the word "martin." It may have been derived from the Irish and Gaelic "mart" meaning heifer or cow. Efforts have been made to trace it to St. Martin who, according to legend, once cast the devil from a cow. Moreover, St. Martin is said to have been the patron saint of twins and unusual

[1] Received for publication January 12, 1940.

[2] The writers are indebted to F. W. Miller, formerly senior physiologist and veterinarian, Bureau of Dairy Industry, who resigned in 1937, for valuable assistance in obtaining the data on which this study is based.

fecundity. Another explanation offered is that on or near November 11, which was called Martinmas day in Scotland and England, it was customary to slaughter cattle the meat of which was salted for winter use and called martinmas-beef. An early English dictionary referred to martin as "not a true heifer, but an undeveloped male with many of the characteristics of the ox, and generally fattened and killed about Martinmas." It has been suggested further that the freemartin may have been given that designation because its meat was so choice that it was reserved for St. Martin's—a great feast day. Moreover the words "mart," "maert," "mert," and "mairt" appear to have been used in Scotland and parts of England in referring to the cow or ox fattened for slaughter and salted or smoked for winter use. Hart (*32*)[3] showed that it is not difficult in view of these facts, to imagine such an individual being referred to as the "farrow-mart-one," or in Scotland as the "farrow-mart-yin," either of which might have been corrupted or shortened into "freemartin."

Despite the general knowledge of the existence of the freemartin condition in cattle and the various notions concerning it that had prevailed through the centuries, Hunter (*37*) appears to have been the first (1779) to place detailed anatomical descriptions of the freemartin on record, and many of the articles published on the subject during the last 150 years have made specific reference to John Hunter's freemartin as a basis for comparison. Most of the early publications were limited chiefly to descriptions of its appearance, sexual behavior, and morphology. In recent years, however, its occurrence has attracted the interest of biologists, embryologists, and geneticists.

Most writers on the subject have held to the theory that the freemartin, which resembles the female more than the male externally, is a modified female. Some have appeared to be uncertain as to its genetic origin, and others have contended that it is a modified male. It is not surprising that opinions should differ on this point because some freemartins having the external appearance of females have been found to be almost devoid of internal genitalia, whereas others of similar external appearance have been found on dissection to possess essentially all of the male genitalia in modified form.

Another question having an important bearing on the matter of genetic origin is whether the individuals in multiple births involving freemartins develop from the same ovum or from separate ova. If both originate from 1 ovum, the freemartin presumably must be a modified male as identical twins are always of the same sex. Hart (*33*) and Cole (*6*) contended that the freemartin and its twin result from a division of the male zygote. Gowen (*22*, *23*) on the other hand, concluded that identical twins do not occur in cattle. However, Kisslowsky (*42*), Kronacher and Sanders (*45*), Kronacher and Hogreve (*44*), Kronacher (*43*), Lush (*52*, *53*), and Jewell (*39*) have offered fairly convincing evidence that identical twins may occur in cattle. Lillie (*47*), in his studies of twin embryos in a packing house, proved almost beyond question that when a single fetus occurs only 1 corpus luteum is present and that almost invariably when twin fetuses occur 2 corpora lutea are present as evidence of the liberation of 2 ova—1 from each ovary—regardless of the sex of the fetuses. Lillie (*50*) showed that in 127 cases of twinning where the maternal ovaries

[3] Italic numbers in parentheses refer to Literature Cited, p. 620.

were available for examination, 126 showed 2 corpora lutea, and that in every case involving two-sexed twins 2 ova had been concerned. Most of those who claim the existence of identical twins in cattle admit their rarity. Evidently monozygotic twinning in cattle is the exception rather than the rule.

EXPLANATION OF FREEMARTINISM

Lillie (*46, 47, 48, 49, 50, 51*), who examined a large number of twin fetuses in a packing house, offered a theory explaining the occurrence of the freemartin in cattle which has been rather widely accepted. More than 96 percent of the bovine twins he examined were monochorial (inclosed in a common placenta); the two fetuses usually had developed in such a way that the blood vessels of the two circulations were joined and a constant interchange of blood had taken place between the two developing fetuses. If both fetuses were male or both were female neither was detrimentally affected by this common circulation, but if one was male and the other female a sterilization of the female took place. In some such cases the development of the female reproductive organs was suppressed, and in extreme cases certain male organs developed in the twin that was originally female. He explained the occasional occurrence of fertility in the female of mixed twins on the theory that, even though monochorial, the vascular systems of the two fetuses do not necessarily become joined.

Although Lillie is usually credited with having performed the original research work leading to the conclusions outlined, he (*49*) gave credit to Tandler and Keller (*63*) for having anticipated certain of his observations. Tandler and Keller found that twin cattle fetuses were inclosed in a common chorion and usually had a joint circulatory system resulting in typical freemartin genital organs in the female if the twins were originally of opposite sex. Nevertheless, for purposes of brevity the foregoing explanation of the cause of the freemartin will be referred to in the following discussion as Lillie's theory.

The histological studies of Lillie's specimens by Chapin (*4*) showed that the interstitial cells of the testis, the secretion of which supposedly determines the development of secondary sexual characters, are produced earlier in fetal life than the corresponding cells of the ovary. Thus, in the case of vascular fusion in mixed twins the sex hormones of the male fetus pass into the circulation of the female embryo early enough to interfere with the development of the mechanism controlling female secondary sexual characters, and the sex organs of the female, which are in an indifferent stage, develop toward the male condition. Chapin attributed the great variation in the degree of alteration or reversal in the reproductory organs of the freemartin to differences in the stage at which the interstitial secretions of the male are introduced into the female embryo, and to the amounts introduced.

Buyse (*3*) attributed the extreme modification he found in a 2½-year-old Brown Swiss freemartin to the fact that it was one of triplets of which the other two were males. However, Pearl (*55*) showed that one male of triplets was capable of sterilizing two females. Similar results were shown by Bissonnette (*2*). Hutt (*38*) cited a case of bovine quadruplets in which one male apparently modified three females and caused them to become freemartins. Lillie (*51*) and

Bissonnette (*2*) concluded that the amount of hormone does not determine the degree of sex modification but that it is an "all-or-none" reaction as far as freemartin formation is concerned. The extremely small quantity of the hormone required to transform the female into a freemartin is particularly noteworthy. Lillie (*51*) showed that in one case a male fetus weighing less than 4 gm. had produced male hormones sufficient to bring about a practical inversion of the ovary in the female twin.

NUMBER OF FREEMARTINS STUDIED AND METHODS EMPLOYED

Reports of the occurrence of the freemartin condition in cattle are too numerous to discuss in detail. Much of the work has been carried on with embryos obtained at slaughterhouses. Other studies have been based on living animals ranging up to several years of age. Many of the reports on record have been based on the study of a small number of individuals. Most of the cases were associated with twins but at least 2 reports involved triplets, and 1 report described freemartinism in connection with the birth of quadruplets. Magnusson (*54*) examined 66 freemartins, most of which were 2 to 3 years of age, and described 11 of them in detail. Lillie (*51*) gave some idea of the large number observed in crediting Keller and Tandler with 91, Lillie with 39, Numan with 8, and Luer with 113. These studies have shown a very marked variation in degree of sex modification.

FREEMARTINISM IN OTHER SPECIES OF ANIMALS

Sex intergrades are known to occur in many species of mammals. Numerous cases of intersexuality closely simulating freemartinism have been found in the goat. Davies (*17*) described a number of cases of what he called caprine freemartins. These animals generally have a tendency to be female (sometimes even being effeminate looking early in life) but become strongly masculine in appearance toward the end of the second year. According to Davies the abnormality is believed to occur in at least 2 percent of goats and appears more frequently in some breeds than in others. He stated that apparently 2 intersexual kids never occur at the same birth, and indicated that in goats the condition may be found (1) in single births, (2) as twin to a normal male, (3) as twin to a normal female, (4) as 1 of triplets with normal male and female, and (5) as 1 of triplets with 2 normal males. One case examined in detail by Davies was described as "exactly similar to the condition described by John Hunter in freemartins in cattle." Rickards and Jones (*58*) also described twin goats that appeared to be typical females at birth, in which the anatomical structure later became strongly masculine although the mammary development appeared to be normal for the female. A study of 25 similar cases in goats was reported by Crew (*7*), whose description was nearly the same as that of Davies and of Rickards and Jones.

Apparently the occurrence of sex intergrades is less frequent in sheep than in cattle or goats. Strebel (*61*) gave figures which indicate that sterility is almost as likely to occur in the ewes of like twins as in ewes twinned with males, and by no means as likely to occur in sheep as in cattle when the twins are of opposite sex. Fraser-Roberts and Greenwood (*19*) reported in detail on a ewe lamb with testicles, which

they considered to be similar to the freemartin. Hunter (*37*) referred to the frequency of sex intergrades in sheep and described them in some detail. Numan, according to Hart (*32*) described intersexuals in both goats and sheep. Lillie (*50*) referred to the frequency of chorionic fusion and the infrequency of vascular fusion. Fincher and Williams (*18*) stated that the chorionic fusion without vascular fusion is the rule in both sheep and goats, and that sometimes vascular anastomosis occurs and occasional asexual young are recorded. Williams (*64*) referred to the citation of one case of limited vascular anastomosis in the ewe. Crew (*7*) reported a case which he stated was very similar to 34 other cases in the goat, the pig, the horse, and in cattle. Gurlt, according to Hart (*32*), concluded that intersexuals in both goats and sheep are analogous to the freemartin.

Hunter (*37*) indicated that intersexuality in the horse is very frequent. He described one case in which the testicles had descended and appeared like an udder. According to Hart (*32*), equine hermaphroditism was reported by Gohier, and by Wotton in 1841, and also by Sebald. Crew (*7*) mentioned two cases of intersexuality in the horse very similar to the intersexual individuals found in the goat, the pig, cattle, and sheep.

Sex intergrades appear to be fairly common in swine. Kingsbury (*41*) described in detail a case in a pig 9 months of age. Lillie (*50*) stated that in swine the fetal membranes often fuse but that vascular anastomosis occurs only exceedingly rarely. Hughes (*36*), however, reported extensive studies of 400 pig uteri of which 4 showed fusion of fetal membranes and vascular intercommunication with abnormalities in the sex equipment of one or the other component twin. Three of the cases were heterosexual. In the fourth both were males. She stated that females of the heterosexual pairs would undoubtedly have developed into typical sterile freemartins such as occur in cattle. Cohrs (*5*) observed a number of cases of different types of embryonic fusion and different degrees of vascular anastomosis. Fincher and Williams (*18*) described a six-fetus chorion in which 4 were males and 2 were perfect females. Abundant vascular anastomoses between the 6 fetuses of mixed sex had failed completely to injure or delay the physiological development of the reproductive system of the females. Crew (*7*) indicated a close similarity between the intersexuals of swine and those of horses, cattle, sheep, and goats, but later (*8*, *10*) appeared to be uncertain as to the analogy between freemartinism in cattle and the intersexual condition found in other species.

Sex intergrades have been observed in still other species. Hunter (*37*) described one in the ass, Crew (*9*) one in the camel, and Hartman (*34*) and Hartman and League (*35*) one in the opossum. Many other cases of sex reversal and sex modification have been reported, several of which were in connection with studies in poultry.

The wide divergence of opinion with regard to the analogy between freemartinism in cattle and intersexuality in other species has been pointed out. Some investigators have shown placental and vascular anastomosis combined with anatomical abnormalities in a number of different species that appeared to be similar to those in cattle, and claim they are practically identical. Others, like Lush (*52*), state that the freemartin "does not appear to exist, or at least is rare among

twins in horses, sheep, goats, and other mammals." It seems probable that, if typical freemartinism does occur in other mammals it is the exception rather than the rule, whereas in cattle it is the rule when twins of both sexes are born.

HERMAPHRODITISM IN THE HUMAN

The observation of freemartinism in cattle naturally led to legendary beliefs with regard to its occurrence in humans. Some degree of hermaphroditism supposedly occurs about once in 1,000 humans. Many causes appear to exist. Young (*66*) who made an exhaustive study of the manifestations and causes of genital abnormalities in humans indicated that the condition is not associated with twinning and that it is not analogous to the freemartin condition in cattle. Simpson (*59*) found that in 113 cases of human mixed twins 103 of the women had families. When he included several cases of triplets and 1 of quadruplets the total number of women was increased to 123, of whom only 11 failed to have offspring. This ratio of unproductive individuals was slightly less than the ratio found in his study of 1,252 marriages, of which 146 were without offspring. He found also that the number of offspring was as great for women born twin with males as for women born singly. It is extremely doubtful if the human sex intergrade is analogous to the bovine freemartin, as it appears that no authentic case has ever been found.

EXPERIMENTALLY PRODUCED SEX INTERGRADES

Strong experimental evidence supporting Lillie's theory that freemartinism is caused by the influence of male hormones, has been presented recently by Greene and Ivy (*28*) and by Greene, Burrill, and Ivy (*24, 26*) who showed that testosterone or testosterone propionate (male sex hormones) when injected into pregnant rats resulted in a high frequency of abnormal females in the offspring, the abnormalities closely resembling those of the bovine freemartin. The degree of modification appeared to depend on the stage of pregnancy when injected and on the quantity of hormone administered. These authors appear to believe the condition developed is analogous to freemartinism. Raynaud (*56*), Hamilton and Gardner (*30*), and Hamilton and Wolfe (*31*) largely confirmed these results with mice and with rats. Dantchakoff (*12, 13, 14, 15, 16*) obtained similar results with guinea pigs, and showed that the hormone from the adult testicle is identical with that causing the freemartin in cattle. Greene, Burrill, and Ivy (*27*) have shown also that injections of female sex hormones into pregnant rats are capable of producing feminized males. The same authors (*25*) have found that the male sex hormone will cause masculinization when injected into the newborn rat, and Raynaud and Lacassagne (*57*) have shown that sex modification results in the mouse from the injection of either male or female hormones in the newborn or the adult.

MAMMARY DEVELOPMENT, ENDOCRINE ABNORMALITIES, AND OTHER CHARACTERISTICS OF THE FREEMARTIN

The dearth of specific references concerning mammary-gland structure in freemartins has been particularly noticeable. Those found have been of a very general nature. Hunter (*37*) described a 5-year-old freemartin in which "there were four teats, the glandular

part of the udder was but small," and a 3-to-4-year-old freemartin in which the teats and udder were small compared with those of a heifer. Scarpa in 1784, according to Ballantyne (*1*) stated that the freemartin resembled a bull but that under the abdomen were mammary glands and teats. Numan in 1829, according to Hart (*32*) described a case in which there was no trace of an udder, the skin in that region was lax and pendent like a sac, and the teats were of the same size as those of a bull. Lillie (*47*) stated that the mammary gland is almost invariably of the female type. Crew (*10*) described the mammary development of the freemartin as similar to that of the immature female and quoted Hartman and League (*35*) as crediting the freemartin with having an udder. Bissonnette (*2*) described the udder rudiments (in bovine fetuses) as apparently normal for females of such kind and size. Galli (*20*) spoke of mammary glands as often absent. Buyse (*3*) stated that no udder was present and the teats were no longer than those found ordinarily in normal bulls. Davies (*17*) referred to the teats of an intersex goat as rudimentary; Rickards and Jones (*58*) described a goat in which the nipples and mammary glands were normal, and its twin in which a scrotal pouch under the site of the mammary gland produced an elevation of the udder making it appear well-developed and normal. Hunter (*37*) mentioned a similar condition observed in an intersex horse. Curson (*11*) seems to have been the only one to go so far as to illustrate the external view of the excised udders of two freemartins. No detailed descriptions of the mammary-gland structure in the freemartin have been found.

Still less information is found regarding the endocrine glands in the freemartin. Young (*66*) and Glynn (*21*) found some associations between endocrine dysfunction and sex malformations in the human. Davies (*17*) stated that the adrenals and thyroid of an intersex goat were undisturbed; Hart (*33*) found that the thyroid, thymus, and suprarenals of a freemartin were normal; and Crew (*7*) found no endocrine disturbance in well-grown intersexual animals, except in the sex glands.

References to the body form of freemartins are few in number. Keller (*40*) showed that freemartins were taller in relation to length than normal heifers, resembling spayed heifers in this respect; that the increased height was due almost entirely to lengthening of the long bones, chiefly the metacarpus; and that freemartins showed prominent withers resulting from elongation of the spinous processes of the vertebrae, a greater horn development, and peculiarities in pelvic form. Numan in 1829, according to Hart (*32*), described a freemartin as resembling an ox in conformation with long, narrow head and long, wide horns. He also said that it had a large, broad, high body, with small bones, and stood high on its limbs. Ballantyne (*1*) referred to a letter in which a farmer expressed existing ideas by describing a certain woman as "just like a freemartin, and had no hips at all." Fincher and Williams (*18*) referred to a freemartin that was slow in developing, and that attained only 70 percent normal size after 1 year.

The enlarged clitoris has often been mentioned in connection with the freemartin. Williams (*65*) showed that, whereas both the female and the male in cattle assume a characteristic pose when urinating, the neuter assumes no such pose beyond the elevation of

the tail. Hunter (*37*) described the bellow of the freemartin as similar to that of the ox, and not at all like that of the bull. Davies (*17*) stated that the caprine freemartin assumed a male position when standing, but that the shape of the head and body resembled the female. Other observers of intersex goats have commented on their habits and the fact that their appearance became increasingly masculine with advance in age. Fincher and Williams (*18*) failed to find typical escutcheons in the bovine asexuals studied and suggested that deviations in the escutcheon may signify teratological aberrations in the internal female genitalia.

PROPORTION OF NORMAL BREEDERS AMONG THE FEMALES OF MIXED TWINS IN CATTLE

Although it has long been recognized that occasionally a female born twin with a bull is normal sexually and therefore is not a freemartin, data are exceedingly fragmentary with regard to the frequency with which such normal cases occur. Strebel (*61*) reported finding 1 normal female among 8 females twinborn with bulls, indicating that 12.5 percent were normal. It is noteworthy that this fertile female gave birth to a sterile heifer. Williams (*65*) indicated that the frequency of normal cases is approximately 1 in 7; Spencer (*60*) referred to 11 cases of which none was capable of reproduction; and Lillie (*51*) summarized his own data and those of others as follows:

Source of data:	*Ratio*
Keller and Tandler (6 normals in 91)	1:15.2
Lillie (6 normals in 39)	1:6.5
Luer (6 normals in 113)	1:18.8
Numan	1:8.0

The average of the 4 ratios is 1:12.1 meaning that a normal female might be expected once in about 12 times. For the 243 cases in the first 3 groups the ratio is 1:13.5 which means that 7.4 percent of the females born twin with bull calves were normal sexually. It is noteworthy that Lillie's data, which show an exceptionally high ratio of normal to abnormal females, were based on histological studies of embryos and that none ever had an opportunity to prove its ability to become a normal breeder.

PLAN OF STUDY AND PROCEDURE FOLLOWED

In connection with a continuous study at Beltsville, Md., of the relation of the conformation and anatomy of the dairy cow to her producing capacity, the authors have made a detailed analysis of the growth, conformation, anatomy, and mammary structure of the viable females that were born twin to bulls in the Bureau's herd. These female twins were slaughtered at different ages in order to provide a basis for comparing them, at different stages of development, with females that were born singly and that presumably were essentially normal in conformation, anatomy, and sexual development.

The data obtained on growth and conformation consist of the live weight and a large number of body measurements for each animal. The anatomical data include weights and/or measurements of nearly all the internal organs of the body—including endocrine glands, and measurements of the thoracic cavity.

Consideration was given to abnormalities in both the external and internal genitalia. Studies of the udder included comparisons of the degree of mammary-gland development in individual animals at

different ages, and of the structure of the mammary tissue at the time of slaughter.

In view of the large number of freemartins that have been described in detail since the notable work of Hunter (*37*), a complete case history of all the cases on which this study is based is not justifiable. In general the cases studied have followed closely the pattern of those described by others. Wide variations in degree of sex modification have been found. The individual animals have had the external genitalia of the female—with slight modifications in some cases—and the physical appearance of females. The internal genitalia have in most cases been vestigial and in some cases what appeared to be male gonads were present. In one case one testicle was found at a point close to the usual location of the ovary and one descended and lodged on the upper surface of the udder (pl. 1, *A*, *B*). So far as the genitalia are concerned every case observed seems to have fallen within the limits of modification reported by others. In this report no attempt is made to show the genital abnormalities of all the freemartins studied. A single comparison of the internal genitals of freemartin No. 1006 at 18 months 2 days of age (pl. 1 *A*, B,) with those of a normal heifer at 16 months of age (pl. 2) will suffice to show the extent to which a freemartin was found to depart from the normal. The chief purpose of this report is to furnish additional data on certain characteristics of the freemartin that have been discussed by others, and to present results on other points that other investigators have treated lightly or not at all.

ANIMALS STUDIED

Seventeen females born twin with bull calves were studied. Seven were Jerseys, eight were Holstein-Friesians and two were grade Holsteins. Six were slaughtered at approximately 18 months of age, one was slaughtered at 15 months, two at 12 months, one at 9 months, one at 6 months, two at 3 months, and two at 2 months. The other two died at less than 1 month of age.

Table 1 lists the animals studied and shows the breed, the age at death or slaughter, and the herd number and reproduction record of the dam.

TWIN-PRODUCING TENDENCIES IN INDIVIDUAL COWS

There is much in the literature to indicate that, in species that ordinarily bear 1 offspring at each parturition, the tendency to produce twins may be inherited. In this connection some observations with regard to the data in table 1 are noteworthy. Cow No. 667 was herself born twin with a female, and in 8 calvings gave birth to twins of unlike sex 3 different times. One of her female calves born twin with a bull was aborted; the other 2 appear among the freemartins listed (Nos. 1421 and 1485). Cow No. 289 gave birth to twins at 3 different parturitions; at the fourth calving she dropped twin heifers, and at the sixth and seventh calvings twins of unlike sex were born, the females being listed as Nos. 1200 and 1229. Moreover, the autopsy of No. 289 showed that she was carrying twin female fetuses, making her fourth set of twins, 3 of which occurred at successive pregnancies. The fact that 5 of the dams (Nos. 485, 460, 271, 667, and 289) 1 of which was herself a twin, gave birth to 13 sets of twins, might be interpreted as indicating that twinning was an inherited trait in these animals.

TABLE 1.—*Females born twin with male calves, and reproduction record of their dams*

Herd No. of female twin	Breed	Age at death or slaughter	Herd No. of dam	Dam's age when female twin was born	Dam's parturition when twin was born	Sex of dam's offspring at each parturition—									Remarks
						First	Second	Third	Fourth	Fifth	Sixth	Seventh	Eighth	Ninth	
		Yr. Mo. Day		*Yr. Mo. Day*											
691	Jersey	1 6 25	485	7 8 10	Fifth	M	M	M	M	M–F	F	M	M		Carrying mixed twin fetuses at death.
834	Holstein	1 6 16	290	4 1 3	Second	F [1]	M–F	M	M						
624	Jersey	1 6 3	460	6 8 6	Fifth [2]	([3])	([3])	F	M	M–F	F	([4])	M	M [5]	
1006	do	1 6 2	628	4 0 6	Second	F	M–F	F	F	F	M	M			
A–70	Grade Holstein	1 5 29	A–49	2 0 24	First	M–F									Carrying female fetus at death.
296	Holstein	1 5 23	229	8 8 4	Sixth	F [1]	M	F [5]	M	M	M–F				
A–82	Grade Holstein	1 2 28	A–37	4 11 24	Third	M	F	M [6]–F							
1209	Holstein	1 0 11	271	11 0 22	Ninth	M	M	([7])	F	F	M	M [1]	F–F	M [6]–F	
1421	Jersey	1 0 6	667	6 11 13	Fifth	M [5]–F [5]	F	F	F	M–F	M	M	M–F		
806	Holstein	0 8 22	274	3 6 7	Second	M	M–F	M	F	M					
1427	Jersey	0 6 1	679	6 7 4	Fifth	F	M	F	M [5]	M [6]–F	M				
1229	Holstein	0 3 0	289	9 8 2	Seventh	M	F	F	F–F	F	M–F	M–F			Carrying female twin fetuses at death.
1212	do	0 2 28	841	4 2 27	Third	F	M	M–F							
1485	Jersey	0 2 1	667	9 11 15	Eighth	M [5]–F [5]	F	F	F	M–F	M	M	M–F		
1205	Holstein	0 2 0	821	5 0 24	Third	F [1]	M	M–F	F	F	M	F	M		
1408	Jersey	0 0 26	1059	2 3 19	First	M–F	([8])	M	M	F	M				
200	Holstein	0 0 18	289	8 6 20	Sixth	M	F	F	F–F	F	M–F	M–F			Do.

[1] Born dead or died at birth (268 to 290 days' gestation).
[2] Estimated on basis of dam's age at first calving after purchase.
[3] Breeding record not available.
[4] Aborted twins.
[5] Aborted.
[6] Male of twins of unlike sex born dead (270 to 283 days' gestation).
[7] Mummified fetus.
[8] Resorbed fetus.

AGE OF DAM AT THE BIRTH OF FREEMARTINS

Many investigators have found that the incidence of twinning increases with the age of the mother up to a fairly advanced age. Of the 17 females born twin with males (table 1), 2 were born of 2-year-old dams, 1 of a 3-year-old dam, 4 of 4-year-old dams, 1 of a 5-year-old dam, 3 of 6-year-old dams, 1 of a 7-year-old dam, 2 of 8-year-old dams, 2 of 9-year-old dams, and 1 of an 11-year-old dam. Eight were born of dams less than 6 years old, and 9 of dams over 6 years. Counting all twin conceptions on record for the 15 dams listed in table 1, including the twin fetuses carried by 2 of the cows at death, the occurrence of twins at each gestation from the first to the ninth inclusive is 3, 3, 3, 1, 4, 2, 2, 3, and 2. The data presented do not appear to indicate any particular age at which twins of either unlike or like sex are most likely to occur. It is noteworthy, however, that not all the cows lived to have 9 conceptions, although 7 of the 15 had 7 or more. If all had continued breeding through 9 conceptions there might have been a shifting of the incidence of twinning toward a more advanced age. Moreover, the results are based on a highly selected group of dams.

PLACENTAL AND VASCULAR ARRANGEMENT

The data obtained in connection with the twins of unlike sex on which this report is based are too limited to be positively identified as supporting or contradicting the theories propounded by Lillie. It is very difficult to make accurate observations on placental and vascular arrangement after the birth of twin calves, and such data were obtainable in only four cases. The observations in connection with these four cases, as made by an experienced veterinary physiologist, are as follows: No. A–70, a sexually abnormal female, was carried in an entirely separate placenta from that of its male twin, but it was not definitely determined whether or not vascular connection existed; in the case of No. 1209 there were separate placentae connected by blood vessels; in the case of No. 1229 the blood vessels from each fetus led to the same cotyledons but did not otherwise anastomose; and in the case of No. 1408 which was determined on autopsy to be normal sexually, each fetus was in a separate placenta and there was no connection between them.

Autopsies of two pregnant cows in the Beltsville herd (A–40 and 485) provided two sets of twin fetuses of unlike sex for observation. In the case of A–40, both of the 233-day fetuses were in the same placenta and there was anastomosis of the blood vessels. One fetus was a male, and the other was determined to be a neuter. The 131-day twin fetuses obtained from cow No. 485 on autopsy were also in a common placenta and there was anastomosis of the blood vessels. The twins were male and female so far as external manifestations were concerned; but as the fetuses and the placental membranes were preserved unseparated, the matter of sexual normalcy of the female was not determined. Plate 3 shows the placental membranes from cow No. A–40 and the membranes and fetuses from cow No. 485, both of which show vascular fusion. The findings reported do not appear to be contrary to the theory advanced by Lillie except possibly in the case of A–70, for which there is nothing in the notes to indicate that vascular fusion was present.

RELATIVE WEIGHT AND CONFORMATION OF THE FREEMARTIN

Only a few general statements have been found in the literature that refer to the size and external form of freemartins as compared with females of the same breed that were born singly. A summary of the weights and body measurements of the freemartins included in this study is given in table 2. The breed averages shown were determined specifically for this study from data obtained over a period of approximately 14 years on females in the Beltsville herd. In order to minimize the tabulation work, the breed averages were determined on the basis of every tenth animal having weights and body measurements, at ages ranging from 3 to 18 months, inclusive. The sample groups so formed contained 17 Holstein-Friesians and 20 Jerseys.

TABLE 2.—*Live-weight and body measurements of freemartins, and of heifers of single births, at 3 to 18 months of age*

Item of comparison, and age of animal (months)	Jerseys			Holsteins				
					Registered parents		Grade parents	
	Breed average	Freemartin average	Relation to breed average	Breed average	Freemartin average	Relation to breed average	Freemartin average	Relation to breed average
Live weight:	*Pounds*	*Pounds*	*Percent*	*Pounds*	*Pounds*	*Percent*	*Pounds*	*Percent*
3	146	130	89.0	211	175	82.9	142	67.3
6	284	248	87.3	396	334	84.3	296	74.7
12	518	479	92.5	698	608	87.1	581	83.2
18	663	590	89.0	899	761	84.6	720	80.1
Average			89.5			84.7		76.3
Height at withers:	*Centimeters*	*Centimeters*	*Percent*	*Centimeters*	*Centimeters*	*Percent*	*Centimeters*	*Percent*
3	81.62	79.65	97.6	87.75	83.18	94.8	77.17	87.9
6	95.77	93.63	97.8	102.03	98.98	97.0	94.67	92.8
12	110.35	110.40	100.0	117.82	118.03	100.2	111.75	94.8
18	117.35	118.86	101.3	126.71	127.04	100.3	118.50	93.5
Average			99.2			98.1		92.
Height at hips:								
3	84.43	81.63	96.7	92.02	88.10	95.7	78.88	85.7
6	98.41	94.58	96.1	106.68	104.77	98.2	96.17	90.1
12	112.66	110.46	98.0	122.66	123.00	100.3	114.25	93.1
18	119.06	118.42	99.5	130.85	132.25	101.1	120.42	92.0
Average			97.6			98.8		90.2
Height at pin bones:								
3	83.55	80.97	96.9	91.68	86.57	94.4	78.33	85.4
6	97.13	93.43	96.2	105.27	102.00	96.9	95.58	90.8
12	110.68	109.42	98.9	120.50	118.03	98.0	112.09	93.0
18	116.70	116.64	99.9	128.29	126.96	99.0	119.92	93.5
Average			98.0			97.1		90.7
Length (shoulder to pin bones):								
3	84.95	82.41	97.0	92.41	85.19	92.2	78.94	85.4
6	103.62	100.13	96.6	114.27	105.88	92.7	105.19	92.1
12	127.27	124.04	97.5	138.17	131.51	95.2	127.69	92.4
18	139.36	133.82	96.0	152.61	141.00	92.4	141.13	92.5
Average			96.8			93.1		90.6
Total length, withers to pin bones:								
3	69.66	68.63	98.5	75.58	70.25	92.9	67.50	89.3
6	87.50	84.44	96.5	93.42	90.83	97.2	86.75	92.9
12	106.17	104.25	98.2	113.05	111.00	98.2	107.50	95.1
18	114.71	112.08	97.7	125.17	119.00	95.1	113.00	90.3
Average			97.7			95.9		91.9

TABLE 2.—*Live-weight and body measurements of freemartins, and of heifers of single births, at 3 to 18 months of age*—Continued

Item of comparison, and age of animal (months)	Jerseys			Holsteins				
					Registered parents		Grade parents	
	Breed average	Freemartin average	Relation to breed average	Breed average	Freemartin average	Relation to breed average	Freemartin average	Relation to breed average
	Centimeters	*Centimeters*	*Percent*	*Centimeters*	*Centimeters*	*Percent*	*Centimeters*	*Percent*
Length of loin:								
3	18.75	18.50	98.7	19.88	18.55	93.3	18.00	90.5
6	23.84	23.25	97.5	25.25	23.63	93.6	23.25	92.1
12	27.98	27.63	98.7	29.22	28.83	98.7	29.63	101.4
18	29.99	29.83	99.5	31.68	31.13	98.3	30.00	94.7
Average			98.6			96.0		94.7
Depth fore chest:								
3	35.61	34.80	97.7	38.34	36.17	94.3	33.75	88.0
6	44.53	42.77	96.0	47.29	45.06	95.3	43.50	92.0
12	54.93	54.17	98.6	58.65	57.03	97.2	55.13	94.0
18	60.34	59.72	99.0	64.97	62.88	96.8	58.25	89.7
Average			97.8			95.9		90.9
Depth rear chest:								
3	35.51	34.35	96.7	38.60	35.92	93.1	33.25	86.1
6	44.99	43.60	96.9	47.90	45.88	95.8	43.75	91.3
12	55.25	54.00	97.7	58.71	56.78	96.7	56.38	96.0
18	59.59	58.56	98.3	63.79	62.63	98.2	57.92	90.8
Average			97.4			96.0		91.1
Depth paunch:								
3	36.98	35.50	96.0	40.57	38.10	93.9	35.88	88.4
6	46.55	44.73	96.1	50.16	47.50	94.7	47.25	94.2
12	56.41	54.44	96.5	60.40	59.06	97.8	58.75	97.3
18	60.20	58.44	97.1	64.60	63.50	98.3	59.58	92.2
Average			96.4			96.2		93.0
Width of fore chest:								
3	18.35	16.72	91.1	21.83	19.70	90.2	17.75	81.3
6	23.72	21.95	92.5	27.91	25.33	90.8	24.13	86.5
12	31.20	29.02	93.0	35.94	32.22	89.6	33.63	93.6
18	34.80	32.78	94.2	40.28	36.46	90.5	35.50	88.1
Average			92.7			90.3		87.4
Width of rear chest:								
3	25.60	24.40	95.3	30.28	27.85	92.0	26.63	87.9
6	33.92	32.98	97.2	39.28	37.77	96.2	33.84	86.2
12	44.08	41.79	94.8	49.34	47.05	95.4	45.67	92.6
18	48.87	45.36	92.8	53.38	49.92	93.5	47.67	89.3
Average			95.0			94.3		89.0
Width of paunch:								
3	27.73	27.12	97.8	32.72	30.99	94.7	29.46	90.0
6	37.70	36.83	97.7	43.53	41.69	95.8	38.84	89.2
12	49.00	47.00	95.9	54.06	51.86	95.9	53.00	98.0
18	53.75	49.61	92.3	57.76	53.29	92.3	52.92	91.6
Average			95.9			94.7		92.2
Width of hips:								
3	20.83	20.00	96.0	24.32	21.75	89.4	20.25	83.3
6	27.74	26.80	96.6	31.06	29.31	94.4	28.13	90.6
12	37.14	36.06	97.1	40.54	38.17	94.2	37.38	92.2
18	41.53	39.50	95.1	46.35	41.88	90.4	42.00	90.6
Average			96.2			92.1		89.2
Width of pin bones:								
3	13.20	11.70	88.6	16.69	14.96	89.6	12.63	75.7
6	16.71	15.40	92.2	21.47	19.69	91.7	18.25	85.0
12	22.59	21.13	93.5	28.50	25.67	90.1	23.88	83.8
18	25.65	23.00	89.7	33.32	29.00	87.0	30.25	90.8
Average			91.0			89.6		83.8

TABLE 2.—*Live-weight and body measurements of freemartins, and of heifers of single births, at 3 to 18 months of age*—Continued

Item of comparison, and age of animal (months)	Jerseys			Holsteins				
					Registered parents		Grade parents	
	Breed average	Freemartin average	Relation to breed average	Breed average	Freemartin average	Relation to breed average	Freemartin average	Relation to breed average
	Centimeters	*Centimeters*	*Percent*	*Centimeters*	*Centimeters*	*Percent*	*Centimeters*	*Percent*
Width of thurls:								
3	22.63	21.65	95.7	26.91	24.96	92.8	21.63	80.4
6	28.69	27.00	94.1	33.62	32.00	95.2	29.50	87.7
12	35.24	34.06	96.7	41.29	39.42	95.5	37.63	91.1
18	38.56	36.67	95.1	45.74	43.13	94.3	41.25	90.2
Average			95.4			94.5		87.4
Width of loin:								
3	14.44	14.40	99.7	16.87	15.54	92.1	14.25	84.5
6	19.09	18.80	98.5	21.52	20.25	94.1	19.13	88.9
12	24.93	24.56	98.5	27.97	27.00	96.5	24.88	89.0
18	27.63	27.58	99.8	31.88	30.00	94.1	27.00	84.7
Average			99.1			94.2		86.8
Circumference of fore chest:								
3	91.35	87.00	95.2	101.94	95.17	93.4	87.25	85.6
6	113.88	108.90	95.6	125.59	118.75	94.6	113.00	90.0
12	142.75	139.63	97.8	155.85	148.83	95.5	147.00	94.3
18	156.98	151.00	96.2	172.41	164.00	95.1	155.50	90.2
Average			96.2			94.7		90.0
Circumference of rear chest:								
3	102.30	97.80	95.6	115.88	106.75	92.1	105.50	91.0
6	130.23	125.60	96.4	143.65	135.50	94.3	128.25	89.3
12	161.53	156.00	96.6	176.12	168.83	95.9	167.00	94.8
18	175.63	167.67	95.5	190.79	180.50	94.6	177.00	92.8
Average			96.0			94.2		92.0
Circumference of paunch:								
3	109.55	106.00	96.8	123.62	116.25	94.0	114.00	92.2
6	139.78	135.90	97.2	155.15	147.13	94.8	143.00	92.2
12	171.15	166.75	97.4	186.44	180.67	96.9	181.50	97.4
18	184.68	175.00	94.8	198.47	187.75	94.6	187.00	94.2
Average			96.6			95.1		94.0
Length of head (Caliper):								
3	27.77	27.06	97.4	31.33	29.70	94.8	27.63	88.2
6	33.52	32.38	96.6	37.03	36.17	97.7	34.13	92.2
12	39.88	40.00	100.3	44.06	44.00	99.9	41.25	93.6
18	43.18	42.58	98.6	48.25	46.00	95.3	44.25	91.7
Average			98.2			96.9		91.4
Width of forehead (Caliper):								
3	12.03	12.44	103.4	12.77	12.00	94.0	11.75	92.0
6	13.56	14.19	104.6	14.98	13.92	92.9	14.00	93.5
12	15.26	16.92	110.9	16.91	16.13	95.4	16.38	97.0
18	16.13	17.58	109.0	17.86	16.75	93.8	16.50	92.4
Average			107.0			94.0		93.7
Width of head, across eyes:								
3	13.96	13.38	95.8	15.14	14.00	92.5	13.00	85.9
6	16.46	15.94	96.8	17.77	16.38	92.2	16.25	91.4
12	19.08	18.58	97.4	20.50	19.38	94.5	19.63	95.8
18	20.64	19.88	96.3	21.87	20.75	94.9	20.75	94.9
Average			96.6			93.5		92.0
Circumference of shinbone:								
3	10.29	9.50	92.3	12.26	11.38	92.8	10.38	84.7
6	12.15	11.50	94.7	14.24	13.50	94.8	12.88	90.4
12	14.43	14.50	100.5	16.69	16.17	96.9	15.38	92.2
18	15.33	15.00	97.8	18.03	17.50	97.1	16.50	91.5
Average			96.3			95.4		89.7
Average for all items			96.7			94.4		90.0

The extent to which the freemartins differed from the breed averages is more clearly indicated in table 3, which gives the distribution of the average percentages shown in table 2 that represent the proportionate development of the freemartins to that of the breed average.

TABLE 3.—*Distribution of percentages that show the relation of the freemartins to the average for the respective breed*

Breed	Items of body size or measurement in which the relation of the freemartin average to the breed average was—				
	100 per-cent or above	95.0 to 99.9 per-cent	90.0 to 94. 9 per-cent	85.0 to 89.9 per-cent	Below 85 per-cent
	Number	*Number*	*Number*	*Number*	*Number*
Jersey	1	20	2	1	
Holstein:					
Registered		11	11	1	1
Grade			16	6	2

In general the Jersey freemartins were not greatly retarded in development; the Holstein freemartins were definitely undersized; and the grade Holstein freemartins were very much below the Holstein breed average in body size. Undersize was most pronounced in live weight. Apparently, however, the comparatively low weights and measurements of the freemartins did not result from condition of flesh. Deficiency in body size in freemartins seemed to be more pronounced in widths than in the other body dimensions. In other words the freemartins were small, and they were inclined to be narrow in relation to height, length, and depth. The undersize of the grade Holstein freemartins is probably not significant since the grade Holsteins in the Beltsville herd are intensely inbred and the whole population is undersized.

COMPARISON OF FREEMARTINS WITH HEIFERS TWINNED WITH HEIFERS

Since twins usually are below the average in weight at birth the question arose as to whether the freemartins under consideration were undersized because they were freemartins or because they were twins. The twin heifers in the herd that lived to at least 12 months of age were compared with the breed averages used in studying the comparative development of freemartins. Data were available for five Jerseys and two Holsteins. All but one of the seven were measured up to at least 18 months of age.

In live weight the Jersey twin heifers were definitely smaller than the Jersey freemartins at 3 months but had attained greater size than the freemartins at 6 months and remained heavier both at 12 and 18 months of age. However, they did not reach the breed average, the percentages of average weight at 3, 6, 12, and 18 months being 81.5, 91.2, 93.6, and 92.6, respectively; the comparative percentages for the freemartins were 89.0, 87.3, 92.5, and 89.0. For the 23 measurements of body size the average percentages at 3, 6, 12, and 18 months were 93.9, 96.9, 96.4, and 96.7 for the twin heifers as compared with 96.4, 96.5, 98.0, and 97.2 for the freemartins. In skeletal growth both groups were within about 6 percent of the breed average at 3 months and about 3 percent at 18 months.

The two Holstein twins were not weighed or measured until they were 6 months old. They were smaller at 6 months of age than the Holstein freemartins studied. This was especially true for live weight and occurred also for 19 of the 23 items of body measurement. There was a definite tendency for the Holstein twins to approach the breed average with advance in age—nearly or entirely reaching it at 18 months, while the Holstein freemartins remained approximately as far below the breed average at 18 months as at 6 months of age.

Of course, definite conclusions cannot be based on such small groups of animals. Taking both breeds into consideration, however, it appears that not only were the freemartins definitely undersized at the ages represented, but there was a tendency for them to approach the breed average more slowly than heifers twinned with heifers—especially as far as live weight is concerned. It seems probable that the smallness of the freemartins was due to the fact that they were twinborn rather than that they were freemartins.

ANATOMICAL STRUCTURE OF THE FREEMARTIN

Aside from detailed descriptions of the genitalia there is little in the reports of other investigators to show the extent to which the internal anatomy of freemartins departs from the normal. In the present study a comparison of the internal anatomy of freemartins with normal animals of the same breed and age was difficult because of the limited data available on normal animals. The anatomy of the freemartins slaughtered at 2 and 3 months of age was compared with that of bulls because data were not available for normal heifers of these ages. It was necessary also to combine the data for Holsteins with those for Jerseys in some of the groups. Resulting inconsistencies are overcome for the most part by the fact that, except for age and empty-body weight, all comparisons are based on units of weight, or measurements, per 100 pounds empty-body weight rather than on the absolute weights, or measurements, of the organs and body parts compared. Empty-body weight is the difference between the live weight of the animal before slaughter and the weight of the contents of the digestive tract.

Table 4 shows the size of the internal organs and body parts of freemartins and of other dairy cattle of similar age, compared on a basis of the number of units of weight or measurement per 100 pounds of empty-body weight.

The individual percentages which show the relation between the freemartins and the animals used for comparison vary considerably for the different items, and for the same item at different ages. The averages shown in table 4 are based on the individual percentages rather than on the number of pounds, grams, or centimeters per 100 pounds empty-body weight because the latter are not entirely comparable. The average of the percentages for all of the ages represented is given for each item in the last column. The percentage for empty-body weight is only 78.6, which shows that the freemartins were actually much smaller than the animals with which they were compared. In view of the retarded mammary development of the freemartins it is noteworthy that the lowest percentage (81.8) is for weight of udder.

TABLE 4.—*Size of internal organs and body parts of freemartins and of other dairy cattle of similar age, compared on basis of number of units of weight or measurement per 100 pounds of empty-body weight*

Weight or measurements	Unit	2-month group			3-month group			6-month group			9-month group			12-month group			15-month group			18-month group			Average all ages
		Freemartins [1]	Animals used for comparison [2]	Relation of freemartins to animals used for comparison	Freemartins [3]	Animals used for comparison [4]	Relation of freemartins to animals used for comparison	Freemartins [5]	Animals used for comparison [6]	Relation of freemartins to animals used for comparison	Freemartins [7]	Animals used for comparison [8]	Relation of freemartins to animals used for comparison	Freemartins [9]	Animals used for comparison [10]	Relation of freemartins to animals used for comparison	Freemartins [11]	Animals used for comparison [12]	Relation of freemartins to animals used for comparison	Freemartins [13]	Animals used for comparison [14]	Relation of freemartins to animals used for comparison	Relation of freemartins to animals used for comparison
		No.	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*No.*	*No.*	*Pct.*	*Pct.*
Empty-body weight	Pounds [15]	83.00	107.71	77.1	144.48	189.50	76.2	169.05	259.74	65.1	356.65	391.00	91.3	421.37	516.39	81.6	324.45	558.98	58.1	569.19	563.10	101.1	78.6
Live weight	do	112.36	108.94	103.1	112.55	110.82	101.6	117.13	115.38	101.5	135.63	116.37	116.6	114.68	114.04	100.6	118.66	116.25	102.1	113.18	116.80	97.0	103.2
Weight of blood	do	5.24	5.02	104.4	6.22	5.80	107.2	6.09	5.13	118.7	3.90	5.24	66.8	4.46	4.27	104.2	4.99	4.05	109.6	4.24	4.65	116.2	100.4
Weight of thyroid	Grams	8.66	8.07	107.3	10.24	13.56	75.5	5.92	5.19	114.1	6.22	6.14	101.3	4.89	4.46	109.6	4.43	3.68	120.4	3.78	3.78	101.0	111.2
Weight of brain	do	301.73	299.68	116.2	199.29	178.36	111.7	148.46	122.85	120.9	92.48	99.74	92.7	85.89	72.90	118.3	98.65	71.98	137.6	66.33	100.0	100.0	112.0
Weight of pituitary	do	.68	.72	94.4	.61	.61	100.0	.51	.44	115.9	.42	.93	71.0	.32	.39	166.7	.62	.43	183.4	.78	.60	110.0	81.8
Weight of udder	Pounds	.59			.85			.92	.90	102.2	.66	.83	79.5	1.23	1.54	80.2	1.59	1.92	146.3	7.78	8.96	86.8	99.3
Weight of hide	do	8.34	9.37	89.0	7.70	9.13	84.3	8.49	8.67	97.9	7.75	8.80	87.9	8.63	8.54	103.3	2.42	7.64	147.6	1.52	1.44	94.7	112.6
Weight of liver	do	2.16	1.87	115.5	2.17	1.98	109.6	2.54	2.08	128.3	1.97	1.97	97.2	99.84	94.27	97.1	62.66	104.40	66.7	102.93	103.04	99.9	88.8
Weight of spleen	Grams	173.10	155.88	111.1	124.87	165.44	75.5	100.86	108.64	92.8	88.97	124.45	71.7	46.89	46.11	101.7	42.84	45.00	95.2	60.32	46.40	130.0	116.0
Weight of pancreas	do	49.63	41.86	118.6	56.76	43.43	130.7	52.06	54.14	96.2	46.79	54.27	86.2	35.88	29.76	120.5	41.77	29.27	142.7	26.55	29.22	90.9	123.6
Total length of intestines	Feet	117.44	84.15	139.6	76.35	62.30	122.6	81.51	53.31	152.9	41.73	40.55	102.9	35.88	41.77	85.9	29.27	26.55	110.2	23.11	2.52	123.4	2.48	100.8	118.8
Total weight of empty intestines	Pounds	6.08	4.58	145.9	4.36	4.49	97.1	5.65	4.04	139.9	4.06	3.21	126.5	2.32	2.36	98.3	3.11	2.52	123.4	2.48	2.46	100.8	
Weight of rumen	do	1.01	.80	113.5	1.18	1.32	89.4	2.19	1.82	120.3	2.28	1.76	129.6	1.66	1.63	101.8	1.74	1.79	97.2	1.74	1.77	98.3	107.2
Weight of reticulum	do	.21	.23	91.3	.26	.28	98.5	.47	.26	180.8	.29	.27	107.4	.23	.24	95.8	.28	.27	103.7	.31	.29	106.9	110.6
Weight of omasum	do	.23	.22	104.6	.35	.45	77.8	.65	.41	158.5	.46	.40	115.0	.37	.36	102.8	.71	.36	197.2	.45	.41	109.8	129.1
Weight of abomasum	do	.55	.51	107.8	.53	.47	112.8	.29	.30	130.0	.19	.32	126.2	.12	.20	97.5	.56	.41	104.4	.44	.47	99.1	108.0
Total weight of stomachs	do	2.00	1.55	108.1	2.28	2.35	94.8	4.29	3.36	130.8	4.19	3.32	126.2	3.12	3.20	97.5	3.56	3.41	104.4	3.44	3.47	99.1	113.3
Total weight of lungs	do	1.40	1.55	90.3	1.54	1.63	96.2	1.56	1.04	130.8	.91	.97	93.8	.96	.86	111.6	1.34	.86	155.8	.83	.86	96.5	113.3
Weight of heart	do	.60	.64	93.8	.65	.68	93.2	1.36	.47	119.2	.53	.47	112.8	.47	.41	114.6	.54	.37	146.0	.37	.39	94.9	110.2
Weight of kidneys	Grams	221.61	236.77	93.6	223.84	238.89	93.7	212.36	194.85	109.0	139.83	135.29	103.4	128.75	129.54	99.4	195.41	113.85	171.6	104.38	110.02	94.9	109.4
Weight of adrenals	do	3.54	4.26	83.1	3.66	4.01	91.3	4.08	3.11	131.2	2.44	2.40	101.7	2.44	2.65	92.1	3.48	2.45	142.0	2.26	2.47	91.5	104.7

See footnote at end of table.

TABLE 4.—*Size of internal organs and body parts of freemartins and of other dairy cattle of similar age, compared on basis of number of units of weight or measurement per 100 pounds of empty-body weight*—Continued

Weight or measurements	Unit	2-month group			3-month group			6-month group			9-month group			12-month group			15-month group			18-month group			Average all ages
		Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Freemartins	Animals used for comparison	Relation of freemartins to animals used for comparison	Relation of freemartins to animals used for comparison
		No.	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
Weight of dressed carcass	Pounds	55.51	61.57	90.2	60.11	60.16	99.9	53.45	59.18	90.3	61.51	60.91	101.0	59.89	62.64	95.6	56.63	64.03	88.4	61.65	61.33	100.5	95.1
Depth of thoracic cavity at eighth thoracic vertebra.	Centimeters	26.46	20.98	126.1	16.65	13.19	126.2	17.01	11.33	150.1	9.11	8.18	111.4	9.12	7.45	122.4	11.79	7.26	162.4	7.25	7.50	96.7	127.9
Maximum length of thoracic cavity.	do	41.69	33.92	122.9	28.53	23.61	120.8	27.95	19.48	143.5	15.83	14.19	111.6	13.09	11.77	111.2	18.80	11.84	158.8	11.16	11.28	98.9	124.0
Width of thoracic cavity at seventh rib.	do	17.99	14.93	120.5	13.18	10.40	126.7	10.83	8.50	127.4	7.12	6.32	112.7	5.92	5:18	114.3	8.23	5.28	155.9	5.00	5.16	96.9	122.1
Weight of thymus	Grams	119.27	109.04	109.4	212.69	118.10	180.1	162.38	100.42	161.7	51.56	103.84	49.7	107.57	88.24	121.9	8.66	88.16	9.8	53.66	86.70	61.9	99.2
Weight of pineal	do	.19	------	------	.11	.08	137.5	.08	.06	133.3	------	------	------	.04	.04	100.0	.47	.57	82.5	.05	.04	125.0	115.7
Average all items [16]	Percent	------	------	109.0	------	------	108.8	------	------	123.0	------	------	99.2	------	------	106.7	------	------	122.1	------	------	99.1	109.8

[1] 1 Holstein and one Jersey, average age 2 months 1 day.
[2] 3 bulls (2 Holsteins, and 1 Jersey), average age 1 month 27 days.
[3] 2 Holsteins, average age 2 months, 29 days.
[4] 1 Holstein bull, age 3 months 2 days.
[5] 1 Jersey, age 6 months 1 day.
[6] 4 heifers (2 Holsteins and 2 grade Holsteins), average age 6 months 1 day.
[7] 1 Holstein, age 8 months 22 days.
[8] 1 Holstein heifer, age 9 months 2 days.
[9] 1 Holstein and 1 Jersey, average age 12 months 9 days.
[10] 4 heifers (1 Holstein and 3 grade Holsteins), average age 12 months.
[11] 1 grade Holstein, age 14 months 28 days.
[12] 3 grade Holstein heifers, average age 15 months.
[13] 1 Holstein, 1 grade Holstein, and 2 Jerseys, average age 18 months 11 days.
[14] 4 heifers (2 grade Holsteins and 2 Jerseys), average age 17 months 26 days.
[15] Actual values, whereas other items are based on units per 100 pounds empty body weight.
[16] All items except age, empty-body weight, live weight, and the individual divisions of the stomach.

With few exceptions the percentages are above 100. The average of the percentages for all items and for all ages is 109.8. Although the organs and body parts of the freemartins were relatively about 10 percent larger than those of the animals with which they were compared a separate tabulation shows that actually, on an average, they were only 85.7 percent as large. In other words, the organs of the freemartins were actually smaller but they represented a greater percentage of the empty-body weight.

THE PITUITARY BODY

A study of the freemartin would be incomplete without giving some consideration to the pituitary body in view of its important role in connection with the functions of reproduction and lactation. The pituitary body was actually smaller in the freemartins than in the animals used for comparison at all of the ages represented except 9 months. However, table 4 shows that at 2 months the pituitary body was smaller in relation to empty-body weight in the freemartins than in the animals with which they were compared, whereas at 3 months there was no difference. At both of these ages the animals used for comparison were males. At subsequent ages the animals used for comparison were all females. The average for all ages shows that the relative weight of the pituitary body of the freemartins was 12.0 percent greater than that of the animals used for comparison. For the ages at which only females were used for comparison the relative weight of pituitary body was 17.9 percent greater. This shows that the freemartins had a larger number of grams of pituitary body for each unit of empty-body weight than did the heifers of single births, although actually the pituitary bodies of the freemartins were smaller.

Hall (*29*) studied the pituitary bodies of a number of these freemartins and concluded that in cellular structure they were not typical of either the castrated animal or the normal cow, and were intermediate between the two. Evidently this may be taken to indicate a deficiency of gonadal hormones of either sex.

DEVELOPMENT OF MAMMARY-GLAND TISSUE IN THE FREEMARTIN

Examinations of the form and quantity of mammary-gland tissue in the udders of heifer calves in the breeding herd of the Bureau of Dairy Industry at Beltsville, Md., are regularly made by palpation at 2 weeks, and at 1, 2, 3, 4, 5, 6, 9, 12, and 18 months of age. A description of the different stages through which the mammary-gland development passes, and a table of expectancy or standard showing both the stage of development and the quantity of tissue found by extensive studies to represent the average for Holsteins and for Jerseys, has been given elsewhere by Swett and Matthews (*62*). When examinations are made, the relative degree of advancement in glandular development for the individual calf is evaluated on the basis of the standard and is given a grade. Grades range from 1 for the most retarded development to 9 for an extremely precocious one. A grade of 5 is given when the mammary-gland development corresponds to the standard or average for the breed. Grades of 4, 3, 2, and 1

represent progressive degrees of retardation, and grades of 6, 7, 8, and 9 indicate progressive degrees of precocity.

It has been the practice to evaluate the mammary-gland tissue development of freemartins as well as normal heifers. Three of the animals listed in table 1 (Nos. 624, 296, and 806) were examined before the system of assigning grades was adopted, and the degree of mammary-gland development was recorded by means of measurements and descriptive terms. Some of the others were evaluated and given grades at one or more ages before the standard was established. The grades shown in table 5 are those given at the time the udder examinations were made.

TABLE 5.—*Grades for mammary-gland development in females of twins of unlike sex*

Animal No.	Grade assigned at age of—									
	2 weeks	1 month	2 months	3 months	4 months	5 months	6 months	9 months	12 months	18 months
691			2	1	1	1	1	3	3	2
834	5	5	4	1	2	2	2	3	4	4−
1006				4	3	4	5−	5−	4	5
A–70	5		5	2	2+	2	3	5+	4+	4−
A–82	6	5	3	1	1	1	1	2	2	
1209	5	4	3	2−	2+	3	2−	3−		
1421		6	4	5−	4−	4	4+	4−	4	
1427	7	4+		3+	3−	2+	4−			
1229	4−	5+	4+	3						
1212	4−	4	3	2						
1485	7	7	4							
1205 [1]	5	5	8−							
1408 [1]	6									
1200	5									
Average grade [2]	5.33	5.00	3.56	2.40	2.25	2.38	2.75	3.57	3.50	3.75
Average (6 animals) [3]	5.25	5.00	3.50	2.00	2.00	2.17	2.17	3.33	3.40	3.33

[1] Post-mortem examination indicated that animal was sexually normal.
[2] Omitting grades for Nos. 1205 and 1408.
[3] Average grade for the 6 animals (691, 834, A–70, A–82, 1209, and 1421) that had grades extending at least from 2 months to 9 months of age, inclusive.

Up to about 1 month of age the mammary development of the freemartin appears to be about the same as that of the normal female. Since there is very little difference in the mammary gland of the bull and the heifer at 1 month of age, it is to be expected that the freemartin would appear to be normal at that age regardless of any abnormality that might be present in the sexual organs. At 2 months the freemartins were, on an average, below the normal in mammary-gland development. The retardation in mammary-gland development became progressively greater until the age of about 4 months. The resulting decline in grade which occurred in almost every individual case does not represent a diminution in quantity of gland tissue but rather a lack of increase which resulted in a greater departure from a progressively increasing normal quantity. After the age of 4 months there was an upward trend in the average grade which, however, did not at any time reach the level that represents normal development. It is possible that an increase in the mass of tissue resulting from fat deposition, rather than an actual increase in glandular tissue, was to some extent responsible for the higher grades being given at the more advanced ages. A grade of 5 was recorded subsequent to 4 months of age in the case of only two animals. Three

animals that died or were slaughtered prior to 4 months of age showed the typical decline in grade.

The two females born twin with bulls (Nos. 1205 and 1408) that were found at time of slaughter to have normal genital development had grades of 5 or above for mammary-gland development. Grades for these two normal heifers are listed, but are not included in the averages in table 5.

A number of the animals listed in table 5 were slaughtered at an early age and consequently had grades covering only the early stages of mammary development. In order to determine whether these individuals affected the decline and subsequent rise in the average grade, an average was determined for the six animals (Nos. 691, 834, A–70, A–82, 1209, and 1421) that had grades extending at least from 2 to 9 months of age, inclusive. There is no marked difference in the two sets of averages (table 5). Moreover, the three animals that were not originally evaluated in terms of grades and those that were graded before the breed standards were definitely established, have been either graded or regraded on the basis of original descriptions, measurements, and other data in conformity with current standards in order to determine how much the results in table 5 would be affected. The additions and slight adjustments made did not materially change the results.

Not only were the grades sufficiently low to indicate definite retardation of mammary-gland development in nearly all the freemartins over 3 months of age, but there were several cases in which the type of development did not follow the usual pattern. In such cases the glands were irregular in shape, sometimes indefinite in outline, and in certain instances consisted of a nearly shapeless mass of tissue which did not pass through the normal stages of development from birth to maturity. An abnormal mammary-gland development of this sort is called atypical.

At the time of slaughter the udders were removed. Those from the older freemartins were filled with a formalin solution, frozen, and cut into vertical transverse sections according to the procedure regularly employed by the Bureau in studying the gross anatomy of the udders of cows at the time of slaughter. The mammary glands from the very young animals were dissected in such a manner as to show the form and size of the gland-tissue development in at least two quarters.

The comparative development of the mammary-gland tissue in freemartins and in heifers of similar age that were born singly is illustrated in plates 4 to 14, inclusive. They show the structure of the udder in a transverse, essentially vertical plane passing through one of the rear teats. The photographs were all taken at approximately the same scale.

In selecting the heifers whose udders were used for comparison, an effort was made to obtain animals that were of approximately the same age as the freemartins and that were essentially normal in degree of mammary-gland development. The heifers used for comparison had grades closely approximating the average. Three of the seven heifers used for comparison were younger than the freemartins with which they were compared; two were slightly older; and two were approximately the same age.

Table 6 is presented as an aid to a better understanding of the comparisons made. It shows the identity and the breed of each animal; gives the grade, adjusted to standards now in use, to show the relative degree of mammary-gland development; and indicates the capacity of the secretory system of each udder as determined at the time it was filled with formalin in preparation for freezing and subsequent anatomical studies. Although some of the freemartins had grades as high as 4 for mammary-gland development they were in every case below the normal in this respect. The average of all the freemartin grades shown in table 6 is 3.1 whereas the average for the heifers used for comparison is 5.1. The capacities also were consistently lower for the freemartins than for the heifers used for comparison, except in the case of No. 691 for which there are definite indications of error due to pockets of formalin under the skin. The fact that Holsteins are compared with Jerseys in some instances is of little importance as the mammary-gland development of the two breeds has been shown to differ only slightly, on an average, at most of the ages represented (*62*).

TABLE 6.—*Comparative udder capacity of freemartins and of heifers of similar age that had approximately the average mammary-gland development*

Freemartins						Heifers used for comparison					
Animal No.	Age at death		Breed	Antemortem grade for mammary-gland development [1]	Udder capacity	Animal No.	Age at death		Breed	Antemortem grade for mammary-gland development [1]	Udder capacity
	Mo.	*Days*			*Pounds*		*Mo.*	*Days*			*Pounds*
691	18	25	Jersey	2	[2] 9.36						
834	18	16	Holstein	4−	4.00	510 U. S.	17	2	Grade Holstein.	6	7.69
1006	18	2	Jersey	4	6.09						
A-70	17	29	Grade Holstein.	4−	6.51						
A-82	14	28	do	[3] 1−	.26	508 U. S.	14	0	do	6−	8.60
1209	12	11	Holstein	[4] 2	.32	507 U. S.	10	29	do	5+	4.63
1421	12	6	Jersey	4	3.38						
806	8	22	Holstein	3−	1.59	68 U. S.	9	2	Holstein	5	4.86
1427	6	1	Jersey	4−	.32	75 U. S.	6	1	do	6	.50
						1259	6	0	do	4	.91
1229	3	0	Holstein	3	.09	686	3	19	Jersey	4	.55

[1] Grades adjusted to conform to current standards.
[2] Capacity appears to be too high. Photograph shows definite indications of collection of formalin between the skin and the mammary gland (pl. 4).
[3] Graded at 14 months 25 days.
[4] Graded at 9 months of age.

Among the four older freemartins (table 6) the udder of No. 691 was relatively small, and only a very small part of the total consisted of gland tissue. Apparently its total size as well as its capacity was exaggerated by the large pocket of formalin which collected under the skin (pl. 4). Fully half of the area of the section of the udder of No. 834 appeared to be fat, the cistern was small and visible ducts were almost lacking (pl. 5). Nearly the same proportion of fat to gland tissue occurred in the section of No. 1006 (pl. 6), but the duct formation was more complete. It did not differ greatly in appearance from the udders of normal heifers of the same age. There was also a small

proportion of gland tissue in the udder of No. A–70, and the gland tissue was not clearly differentiated from the fat which surrounded it (pl. 7). The udder of No. 510 U. S., apparently a normal heifer, was used for comparison with the udders of these four freemartins. Although she was graded slightly above the average in mammary-gland development, she was younger than any of the four freemartins. Her udder was larger than any of the others except possibly that of No. 1006; the gland tissue was fairly widely distributed and clearly differentiated; and the formation of the teat, the cistern, and the duct system appeared to be typical for a heifer of this age (pl. 8).

A striking contrast is shown in the udders of freemartin No. A–82 and of normal heifer No. 508 U. S. The udder of the former was extremely undersized and did not show any clearly differentiated gland-tissue formation. The udder of No. 508 U. S., however, was well developed and generally typical in form, although this heifer was nearly a month younger than No. A–82 (pl. 9, *A* and *B*).

Freemartins No. 1209 and No. 1421 were both more than a month older than normal heifer No. 507 U. S. The mammary development of No. 507 U. S. was approximately normal for her age, as indicated by the grade of 5+. The section from No. 1209 was very small and consisted largely of fat, although the formation of gland tissue was fairly typical (pl. 10, *A*). The gland tissue in the udder of No. 1421 was fairly well distributed but was small in quantity and not clearly differentiated from the fat, and the udder was small (pl. 10, *B*). The section from No. 507 U. S. was much larger than that of either of the freemartins, the gland tissue was widely distributed and more clearly defined, the cistern was of moderate size, and the duct system was fairly well developed (pl. 11).

Freemartin No. 806 was about 10 days younger than normal heifer No. 68 U. S. whose mammary-gland development appeared to be average for heifers of the same age. There was little difference between the two with respect to proportion of gland tissue to fat. The gland tissue was clearly outlined in each, and the duct system appeared to be more fully developed in the freemartin. The freemartin udder, however, was definitely the smaller (pl. 12, *A* and *B*).

Freemartin No. 1427 and normal heifers No. 75 U. S. and No. 1259 were all within 1 day of the same age. The gland tissue in the udder of No. 1427 was not clearly defined and apparently represented only a small proportion of the total area, although the duct system was fairly well developed (pl. 14, *A*). The udders of the two heifers used for comparison were much larger. In No. 75 U. S., the gland tissue represented a large proportion of the total, it was clearly differentiated, and the duct system was unusually well developed (pl. 13, *A*). In No. 1259 the proportion of gland tissue was much lower, it was well differentiated, and the duct system was fairly well developed (pl. 13, *B*). In the case of these two heifers it may be noted that the former was graded 6 and the latter 4 for relative glandular development.

Normal heifer No. 686 was 19 days older than freemartin No. 1229. The udder of the freemartin was slightly the larger but it contained no clearly distinguishable gland formation (pl. 14, *B*), whereas the udder of No. 686 contained a fairly good-sized area of gland tissue with a cistern and some duct formation (pl. 14, *C*).

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The dissected mammary glands of No. 1205 and of No. 887 are shown in Figure 1, *A* and *B*. Both were within 3 days of the same age when slaughtered (2 months, and 2 months 3 days, respectively). No. 1205 was twin born with a bull but was judged normal as a result of post-mortem anatomical findings. Since she was sexually normal, she was not classed as a freemartin and is not listed in table 6. No. 887 was born singly. Apparently she was normal sexually and approximately normal in mammary-gland development. The udder devel-

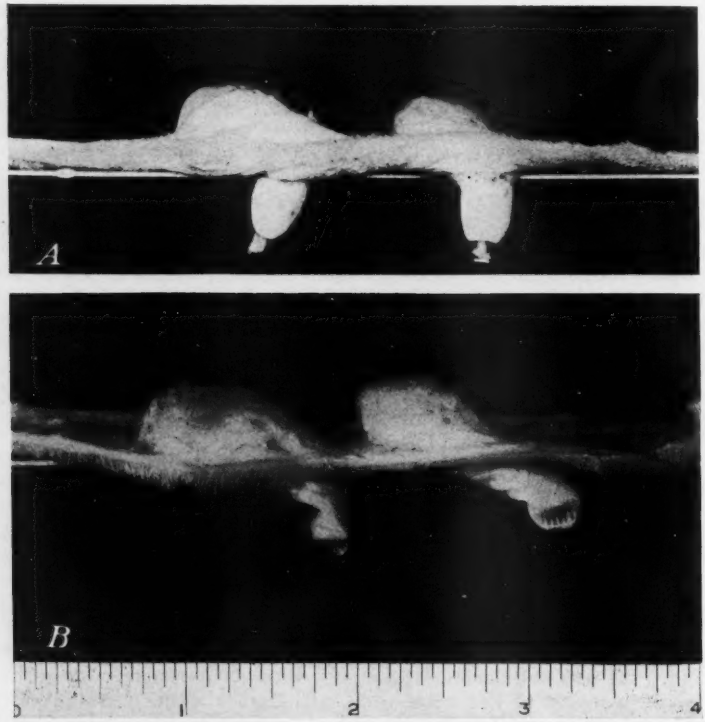

FIGURE 1.—*A*, Dissection showing the mammary-gland tissue development of No. 1205, a normal heifer born twin with a bull (age 2 months); *B*, a similar dissection of No. 887, a normal heifer born singly (age 2 months, 3 days).

opment of No. 1205 was somewhat more advanced, as determined by palpation, than that of No. 887, although the dissections did not indicate any marked difference.

Most of the freemartin udders illustrated contained a comparatively large proportion of fat in relation to gland tissue. In many of the freemartin udders the gland tissue was not clearly differentiated from the fat surrounding it, and in some cases the duct formation appeared retarded in development. In most cases the freemartin udders were relatively small.

CRITERIA FOR RECOGNIZING THE FREEMARTIN AT AN EARLY AGE

The recognition of an early external manifestation of freemartinism will be helpful to breeders since it may save them the trouble and expense of raising females of mixed twins that at breeding age prove to be sterile. There are a number of characteristics that may indicate freemartinism. Possibly one or two of these will be seen in one individual, and other characteristics may indicate this condition in another individual. Following is a discussion of the characteristics that have appeared to be most indicative of freemartinism in the animals included in this study.

The freemartins on which this report is based were undersized and were inclined to be narrow in relation to height, length, and depth. It is very doubtful, however, whether these characteristics were sufficiently pronounced in these animals to indicate freemartinism. The retarded development of these animals probably was due largely to the fact that they were twins.

A definitely retarded mammary-gland development in a female twin born with a bull may be considered as an indication of freemartinism, although too much stress cannot be placed on it because of the wide variation in degree of udder-tissue development in females of single births. Neither is the external appearance of the udder a reliable indication, since the size and shape of the udder and the length and form of the teats vary greatly in heifers born singly.

Probably more credence may be attached to a retarded mammary-gland development that also fails to pass through the typical stages and occurs in an indefinitely shaped mass of tissue that does not conform to the usual pattern.

Another condition frequently, though not always, associated with freemartinism is an enlarged clitoris. Numerous cases have been observed in which the freemartin had external genitals that appeared to be entirely normal. In other cases the clitoris was so much overdeveloped that it was visible at all times and so obstructed the vulva that the urine spurted upward when the animals urinated (figure 2*A* and *B*). Absence of an enlargement of the clitoris is not necessarily an indication of sexual normality but an enlargement is a very good indication that the animal is a freemartin.

One other abnormality that appears to be quite consistently associated with the freemartin condition is the presence of a fold of skin on the median plane of the body, which varies in size and in length but which sometimes extends from the perineum, a short distance below the vulva, to a point close to the navel. In the region of the udder the fold sometimes hangs down to a marked degree. In one freemartin it resembled a scrotum which occasionally was drawn up until it practically disappeared. Usually the fold of skin contains a cord or bundle of fibers, which may be very pronounced in some individuals. Owing to the location of the fold and the enclosed cord it has been referred to frequently as a "rudimentary penis" (figure 3). The dissection of one of these cords led to the conclusion that it was a modified retractor muscle the function of which, in the bull, is to withdraw the penis into the sheath after erection or protusion. In one other case the so-called cord was sectioned for microscopic study.

FIGURE 2.—*A*, The protuding clitoris of freemartin No. 691 at 3 months of age; *B*, the less prominent but greatly enlarged clitoris of freemartin No. 1485 at 2 months of age.

It failed to show an organization of cell structure sufficiently definite to identify it as a rudimentary form of any organ or part. Whatever its origin, it was found in a high percentage of the freemartins studied and was absent in the two females twinned with bulls, that were found on post mortem examination to have normal sexual development.

FIGURE 3.—The prominent fold of skin, sometimes enclosing a cord, which has been referred to as a "rudimentary penis."

ABERRATIONS IN ANIMALS STUDIED

Following is a brief description of the physical and anatomical aberration noted in each of the 17 females twinborn with bulls, on which this study is based.

Jersey No. 691 was extremely retarded in mammary-gland development for a period of several months, at no time approaching the breed average. (See table 5.) The glandular development also was abnormal and was an irregular-shaped mass of tissue. At nearly every observation the clitoris was greatly enlarged and the vulva was very small. The presence of the so-called rudimentary penis was very marked at nearly every examination from 3 to 18 months of age, when the animal was slaughtered. At 12 months of age it extended from the clitoris to the navel and at 18 months it was even more pronounced. Post mortem examination showed only a small outline of the uterus, an absence of ovarian tissue, and a vagina (only about 2 inches long) that did not communicate with the rudimentary uterus. The clitoris was about 1.5 inches long, the vulva opening was only

about 0.75 inch in diameter, and there was a strip of "muscle" beneath the skin that extended from the vulva to the umbilicus.

Holstein No. 834 was very much retarded in mammary-gland development from 3 to 12 months but was improved at 18 months of age. The glandular tissue was a very unusual formation with the tissue very indefinite in shape and outline. The clitoris and vulva, however, appeared to be normal. There was a fairly prominent median fold of skin at 3 and 6 months of age but at 18 months the rudimentary penis was relatively small as compared to that of No. 691. Autopsy showed undeveloped genital organs, no trace of uterus except more dense tissue at that place, and only small nodules in the position usually occupied by the ovaries. The vagina was only about 3¼ inches long.

The data available for Jersey No. 624 show that she was extremely retarded in mammary-gland development, and that the glandular formation consisted of a mass of soft, stringy tissue, which lacked definite shape and outline, which was not typical in any respect, and which was one of the most unusual formations yet studied. Only traces of the usual female internal genitalia were found on post-mortem examination.

Jersey No. 1006 was one of the most unusual cases studied. The mammary-gland development of this animal was only slightly retarded; it adhered fairly closely to the usual pattern with regard to the sequence of stages of development; and at 12 months the internal development was not noticeably different from others of similar age except that the gland was slightly undersized. The clitoris showed no signs of enlargement and the vulva was normal. There was, however, a trace of the median fold or rudimentary penis in this animal. She was found on post-mortem examination to be almost devoid of female genital organs, having only a vagina about 3 inches long and two tubelike structures about 1.5 inches long (similar to the horns of a uterus) that seemed to be continued by strands of tissue for about 12 inches. There were small cysts about the size of immature follicles between these strands. A small rudimentary testicle was found on the right side near the usual site of the ovary. On the left side a similar testicle was found, which had descended and lodged on the dorsal surface of the udder. (See pl. 1.)

Grade Holstein No. A–70 was very much retarded in mammary development at 3 to 5 months of age but showed some improvement subsequently. In type of development of mammary-gland tissue the departure from the normal was comparatively slight. The clitoris and vulva were normal. A median fold containing a cord or rudimentary penis which extended from the rear of the udder almost to the navel was noted at 6, 9, 12, and 15 months of age. It was the dissection of the cord in this animal that led to the conclusion it might be retractor penis muscle. She was somewhat more fully developed internally than most of the freemartins studied, the genitals consisting of small ovarylike glands, uterine horns with tubes to vesicula seminalis, and a vagina about 3 inches long, but she had no cervix (pl. 15).

Holstein No. 296 was very much retarded in mammary-gland development, which appeared to deviate sharply from the usual type. At 9 months it was described as the strangest structure yet observed, at 12 months it had very little similarity to the usual type, and before

slaughter it was described as "not at all typical in shape, or development, or in any other way." No reference was made to the clitoris. At 9 months a layer of tissue hung down between the teats the entire length of the udder along the median line and at the time of slaughter also there were indications of a rudimentary penis. Only the most rudimentary development of the internal genital organs was found on post-mortem examination.

Grade Holstein No. A–82 was extremely retarded in mammary-gland development at from 3 to 6 months of age, after which a slight improvement occurred. At 9 months there were indications of some abnormality in type of mammary development, at 12 months the outline was very indistinct, and at 15 months the gland tissue was indistinct in outline and the quarters were not typical in shape or in position. The clitoris was not enlarged. It may even have been slightly smaller than the average. There was only a trace of the cord elsewhere referred to as a rudimentary penis. Autopsy disclosed a 2-inch vagina, and cordlike tissue leading to tubular uterine horns about 1 inch in length, to which were attached shreds of tissue containing very small bodies that may have been ovaries.

Holstein No. 1209 was very much retarded in mammary-gland development from 3 months on. The mammary tissue was slightly but not significantly atypical or abnormal in form. The clitoris was slightly enlarged at nearly every examination. There was no indication of a rudimentary penis except at 9 months, when a trace was noted. Post-mortem examination showed underdeveloped internal genitalia which included a 3-inch vagina, small seminal vesicles, small tubular structures, and small gonadal lumps resembling testicular tissue.

Jersey No. 1421 was only slightly below the breed average in mammary-gland development, which was typical in form, and the clitoris did not show more than a very slight enlargement at any age. The median cord, however, was noted at 3 months and at each examination thereafter. It seemed to increase in size and distinctness and was most noticeable at the rear and along the udder to its front attachment, but not in the region of the navel. Although the external manifestations were less marked than in some of the others it was predicted that this animal would be a freemartin. On autopsy she was found to be devoid of anything approaching normal internal genitalia and to be a typical neuter.

Holstein No. 806 was definitely retarded in mammary-gland development. At 5 and again at 6 months the formation appeared to be somewhat irregular in type, but at 9 months was described as typical but greatly retarded. There were no notations in the record on the condition of the clitoris; but there was a trace of a narrow fold of skin along the median line at 3 months, although no reference was made to a cord formation within it. Her internal genital organs were markedly vestigial and she was undoubtedly a neuter.

Jersey No. 1427 was definitely retarded in mammary-gland development at 3 to 5 months of age but was more nearly normal at 6 months. There were no indications of abnormalities in the form of glandular development. The clitoris, however, showed a marked enlargement. It was so large that it protruded and was exposed all the time, and the ventral extremity of the vulva pointed nearly straight toward the rear.

At first the rudimentary penis was comparatively small and not very noticeable, but at 6 months it was rather pronounced. Post mortem findings showed only rudiments of the usual female internal genitalia.

Holstein No. 1229 was somewhat retarded in mammary-gland development when slaughtered at 3 months of age. The type of glandular development at that time was described as indefinite and not comparable to others; not conforming to any stage; a soft, irregular mass of fatty and fibrous tissue. In other words it was an atypical mammary-gland development. The enlargement of the clitoris was only slight. The fold and cord were present but not pronounced. Post mortem findings showed that her internal genitals consisted chiefly of an undeveloped vagina, two small bulblike objects in the place of the uterus, and two small lumps at the usual site of the ovaries.

Holstein No. 1212 was very much retarded in mammary-gland development when examined before slaughter at 3 months of age, but there was no indication of abnormality in type of glandular formation. For this animal the outstanding aberration was the greatly enlarged clitoris. It was about 1 inch long, could be seen without opening the vulva, and occupied a very large part of the vulva, which was in nearly a horizontal position. The urine spurted upward and outward on account of the position of the vulva and the obstruction of the clitoris. There was no indication of the co-called rudimentary penis. Post mortem dissections showed that the vulvalike opening continued forward as a diminutive vagina for about 2 inches and ended in a blind pouch. Two testicles with tubes and ampullae were found. The testicles and tubes were in a position similar to that of the ovaries and uterus of the normal female.

Jersey No. 1485 had shown better than average mammary-gland development until just before she was slaughtered at the age of 2 months, when it was slightly below the average and definitely abnormal in form. The clitoris was very pronounced; it was almost fully exposed and was clearly visible from a distance, even at the early age of 16 days. It occupied about one-third of the vulva. There was also a definite indication of a rudimentary penis. At 2 months it consisted of a very pronounced ridge, clearly visible all the way from the rear attachment of the udder to the navel, and containing a small cord which could be detected at almost any point. It was this animal that showed the scrotumlike pouch that was occasionally drawn up until it practically disappeared. Post mortem examination showed that the genitals consisted of small folliclelike structures at the site of the ovaries, fibrous strands instead of a uterus, and a vagina only about 1½ inches long.

Holstein No. 1205 was slaughtered at the age of 2 months. At that time her mammary-gland development was typical in form, and somewhat advanced in degree. The clitoris was not enlarged, in fact it appeared to be unusually small. There was no indication of the median fold or so-called rudimentary penis or of any of the other indications of freemartinism that have been pointed out in the foregoing cases. Post mortem studies showed that she had all of the organs of a normal female and apparently was normal sexually.

Jersey No. 1408 died at the age of 26 days. Only one examination had been made (at 14 days). It did not show any abnormality in degree or in type of mammary development. The clitoris was very

small. No reference was made in the report of the examination to the presence of a rudimentary penis. Autopsy findings indicated that the animal was sexually normal.

Holstein No. 1200 died at the age of 18 days. Only one antimortem examination was made (at 11 days). The glandular development was not notably deficient or unusual in type. The clitoris, however, was very large, very prominent, and visible at all times. It extended above the center of the orifice of the vulva, which stood open above it. There was no indication of the so-called rudimentary penis. The condition of her internal genitals showed that she was undoubtedly an intersexual individual.

Some idea of the extent to which aberrations occur and of their significance may be obtained from table 7. As noted in the discussions, the data for No. 624, No. 296, and No. 806 are incomplete and the absence of a notation does not necessarily indicate that no abnormality occurred. Lack of a notation for any item in the case of the other animals, however, may be considered as a reasonably reliable indication of normalcy for that characteristic.

TABLE 7.—*Physical aberrations noted in 17 females that were twinborn with bulls* [1]

Animal No.	Retarded development of mammary gland	Atypical development of mammary gland	Enlarged clitoris	Presence of rudimentary penis
691	XXX	XX	XXX	XXX
834	XX	XXX	[2]	X
624	XXX	XXX		
1006	X	[3]	[2]	X
A–70	XX	X	[3]	XX
296	XXX	XXX		X
A–82	XXX	XX	[2]	X
1209	XXX	X	X	X
1421	X	[2]	X	XX
806	XX	X		X
1427	XX		XXX	XX
1229	XX	XX	X	X
1212	XXX		XXX	None
1485	X	XX	XXX	XXX
1205 [4]	[3]	[3]	[5]	None
1408 [4]	[3]		[6]	
1200	[3]		XXX	

[1] X indicates that the characteristic occurred as a trace or in a slight degree; XX indicates that it occurred in a definitely marked degree; and XXX that it was very marked or extreme.
[2] Normal.
[3] Approximately normal.
[4] Normal internal genitals.
[5] Advanced.
[6] Very small.

A retarded development of the mammary-gland tissue was the most frequently observed abnormality. It was noted in 14 cases. The presence of the median fold of skin between the vulva and the navel, which sometimes enclosed a cord and which was referred to as a rudimentary penis was noted in 12 cases. An atypical form of mammary-gland development was noted in 10 cases and an enlarged clitoris in 8. Some of the freemartins showed definite abnormalities in 1 or 2 characteristics; some in different ones. Others, like Nos. 691, 1209, and 1229 were abnormal in each of the 4 characteristics. Every 1 of the 17 animals showed at least a trace of 1 or more abnormalities except Nos. 1205 and 1408, both of which appeared on post-mortem

examination to be sexually normal. The 15 that showed ante-mortem manifestations of abnormality were all found on post mortem to be deficient in their internal sex equipment.

The contrast in development of internal genitalia between the apparently normal No. 1205 and the freemartin No. 1485 is shown in plate 16, *A* and *B*.

SUMMARY AND CONCLUSIONS

For some 2,000 years cattle breeders and investigators have observed that a female calf twinborn with a bull calf is likely to be deficient in sexual development and incapable of reproduction. An animal so born and showing such deficiencies is called a freemartin. Investigators have reported fairly conclusive results indicating that such an individual is genetically a female that has developed from a separate ovum and that the sex modification has resulted from the effects of hormones produced by the gonads of the male twin embryo, which have circulated through the female embryo as a result of fusion of the blood vessels of the two placentas.

Sexual aberrations similar to those found in the freemartin are sometimes observed in other than the bovine species. Sex intergrades resembling the freemartin have been produced experimentally in laboratory animals by injections of sex hormones either into the mother or into the embryo. If freemartinism occurs naturally in connection with multiple births involving both sexes, it appears to be the exception in other species whereas in cattle it is the rule. Authorities differ in opinion as to the frequency of occurrence of normal individuals among heifers that are twinborn with bull calves. An average of the estimates given by such authorities indicates that a normal female may be expected about once in 12 cases of twinning involving both sexes.

This report is based on a study of 17 heifers twin born with bulls. All of those that were kept to breeding age proved to be sexually abnormal and incapable of reproduction. A very wide range in degree of abnormality was found. In some the female internal genitals were modified, in some they were almost lacking, and in some male gonads were found. Only 2 of the 17 were found on post-mortem examination to have normal genital development. As these 2 were 2 months of age or less at the time of death it was, of course, not certain that they would have been capable of reproduction at breeding age despite the apparent normalcy of their genital organs.

Although the data are too limited to warrant definite conclusions, twinning appears to have been habitual in some of the dams of the freemartins studied. Among the dams of the freemartins there was no particular age at which twins of either like or unlike sex seemed most likey to occur.

On an average the freemartins were definitely undersized, especially in live weight. Deficiency in body size seemed to be more pronounced in width than in other body dimensions. Although on an average they were undersized at all of the ages studied, there was a slight tendency for the freemartins to approach their respective breed averages more slowly than did heifers twinned with heifers—especially in live weight. The smallness of the freemartins probably was

due to the fact that they were twinborn rather than that they were freemartins. It is very doubtful that either smallness of the individual or any peculiarity in body conformation could be used as a satisfactory basis for distinguishing between freemartins and normal heifers.

On an average the relative size of the organs and body parts, expressed in number of units of weight or measurement per 100 pounds empty body weight, was approximately 10 percent greater for the freemartins than for the animals with which they were compared. Actually the freemartins had the smaller organs. The greater relative size of their organs was due to the fact that the freemartins were more undersized in body weight than in the size of their organs.

The pituitary body was actually smaller in the freemartins than in the animals used for comparison. On the basis of number of grams of pituitary body per unit of empty-body weight, however, the freemartins had the larger pituitary bodies. The freemartin pituitaries that were studied cytologically proved to be intermediate between the condition found in the castrated bovine and that of the normal cow. Presumably this indicates a deficiency in both the male and female sex hormones.

The mammary-gland development of the freemartins as determined by palpation was, on an average, approximately normal up to about 1 month of age after which it was definitely retarded. The greatest retardation occurred at about 4 months after which there appeared to be a tendency for some improvement.

The udders of the freemartins had lower capacities than the udders of normal heifers of the same age, in most cases they contained a high percentage of fat in relation to gland tissue, in many of them the gland tissue was not clearly differentiated from the surrounding fat, and in some the duct formation appeared to be retarded. In most of the freemartins the udders were relatively small.

There are a number of characteristics that appear to be indicative of freemartinism and useful in determining whether or not any given female twin born with a bull calf is likely to be capable of reproduction. Many of the freemartins included in this study were greatly retarded in udder development. In some cases the mammary-gland development was atypical. Another characteristic found in many of the freemartins was an enlarged clitoris; and still another which was very often present was a fold of skin, sometimes containing a cord, which extended along the median plane of the body, part or all of the way from a point above the rear attachment of the udder to the navel. This has been referred to in this study as a "rudimentary penis." In some freemartins all of these characteristics occurred. In others only 1 or 2 could be detected. One or more was found in everyone of the 15 cases studied that proved on autopsy to be deficient in sexual development. None was found in either of the 2 that had normally developed internal genital organs at the time of death.

The chances are slight that the heifer twinned with a bull will be sexually normal. In some cases positive determination probably cannot be made until the animal reaches breeding age. However, if one or more of the abnormalities described are present it probably will be good economy to dispose of the animal.

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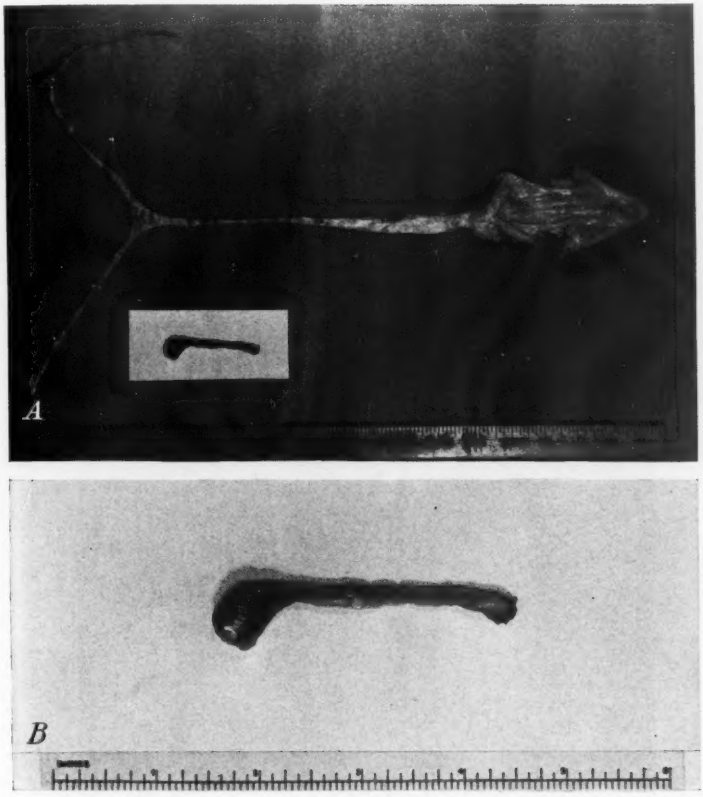


Internal genitals of freemartin No. 1006 at 18 months 2 days of age: *A*, The genital tract; *B*, the descended testicle.

Internal genitals of normal heifer No. 509 U. S. at 16 months of age.

A, Vascular fusion of twin bovine fetuses of cow No. A–40: *a*, Umbilical cord of one fetus; *b*, umbilical cord of the other; *c*, direct vascular connection between them. *B*, Twin bovine fetuses of unlike sex from cow No. 485 showing vascular fusion.

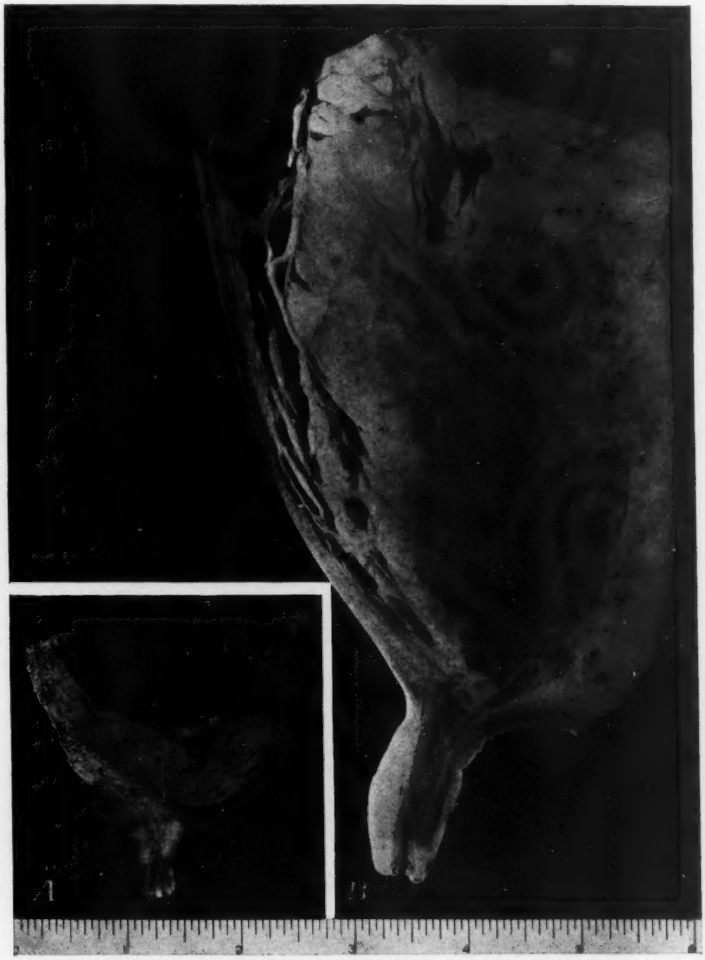
Section through a rear quarter of the udder of freemartin No. 691 at 18 months 25 days of age.

Section through a rear quarter of the udder of freemartin No. 834 at 18 months 16 days of age.

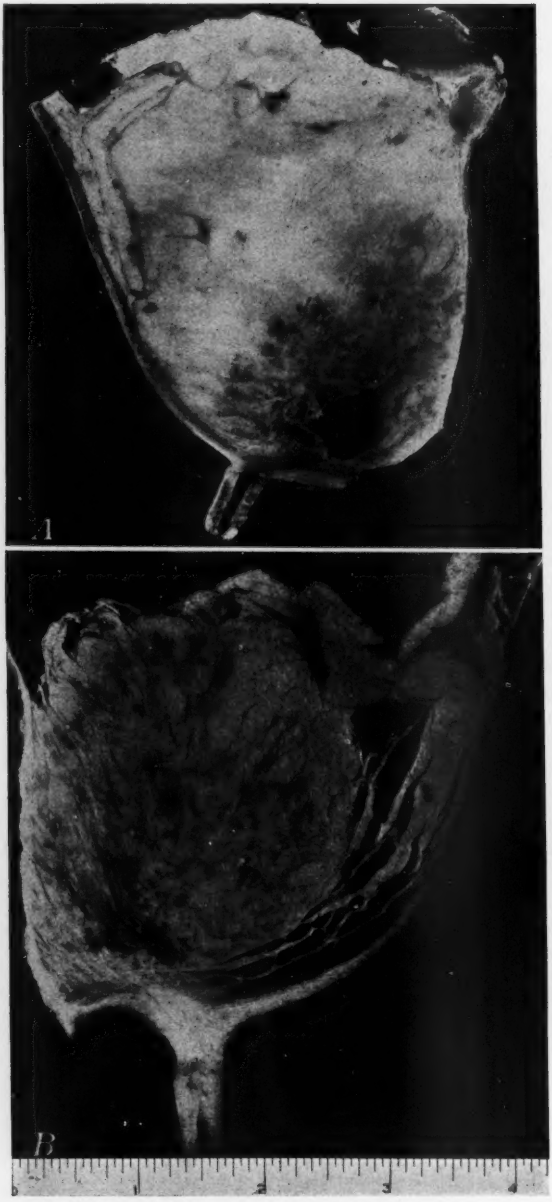
Section through a rear quarter of the udder of freemartin No. 1006 at 18 months 2 days of age.

Section through a rear quarter of the udder of freemartin No. A–70 at 17 months 29 days of age.

Section through a rear quarter of the udder of normal heifer No. 510 U. S. at 17 months 2 days of age.

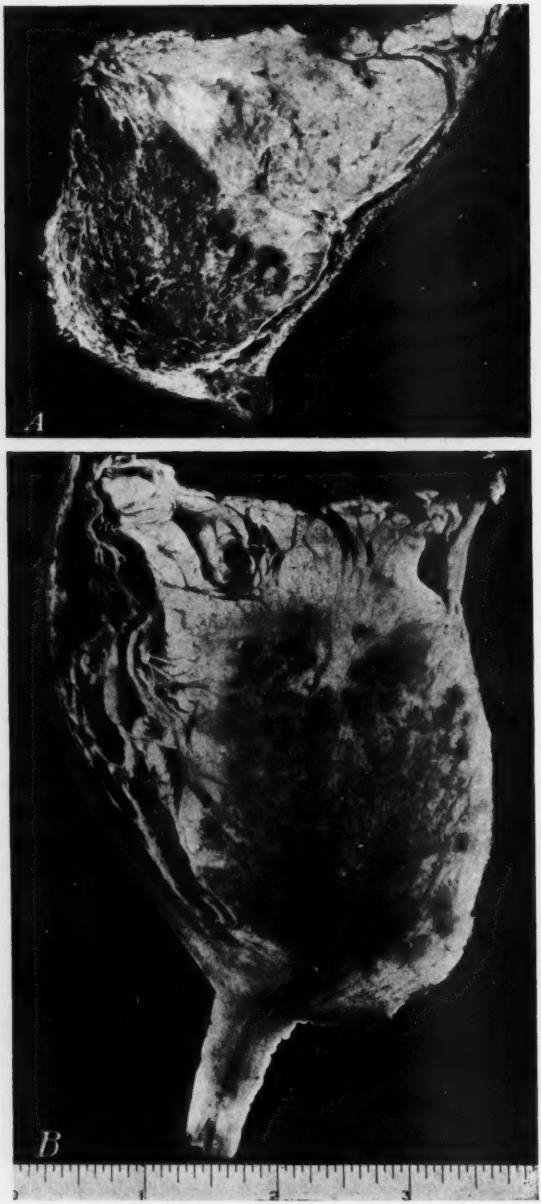


A, Section through a rear quarter of the udder of freemartin No. A–82 at 14 months 28 days of age; *B*, section through a rear quarter of the udder of normal heifer No. 508 U. S. at 14 months of age.

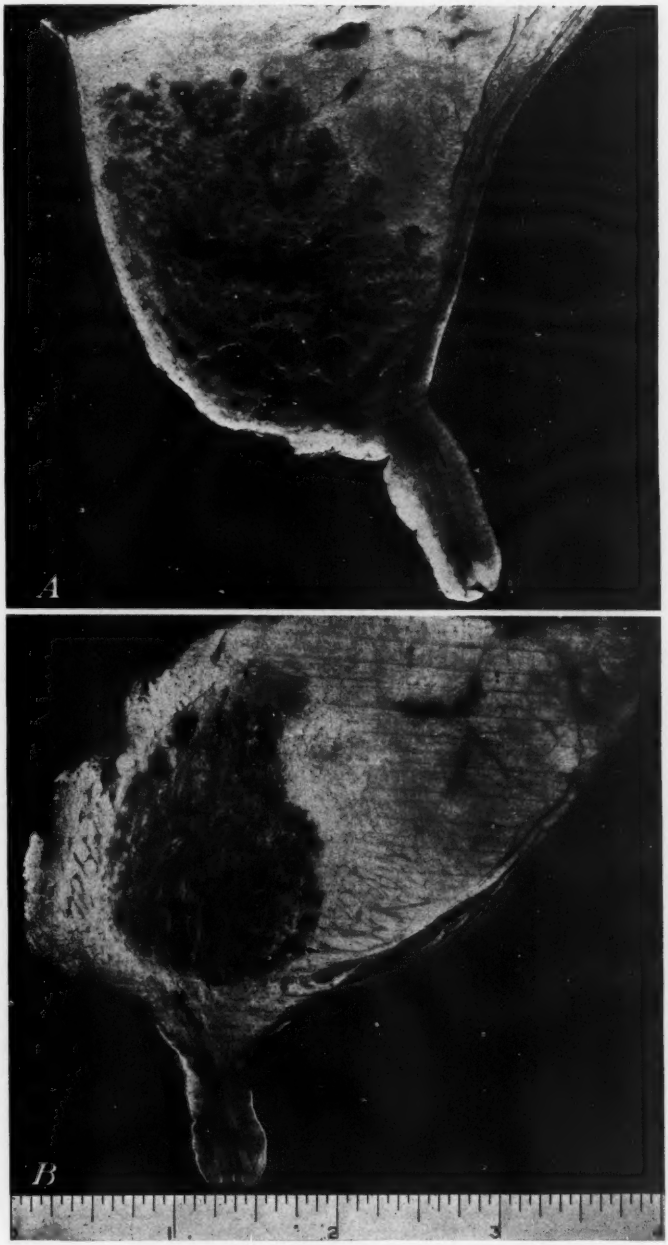


A, Section through a rear quarter of the udder of freemartin No. 1209 at 12 months 11 days of age; *B*, section through a rear quarter of the udder of freemartin No. 1421 at 12 months 6 days of age.

Section through a rear quarter of the udder of normal heifer No. 507 U. S. at 10 months 29 days of age.



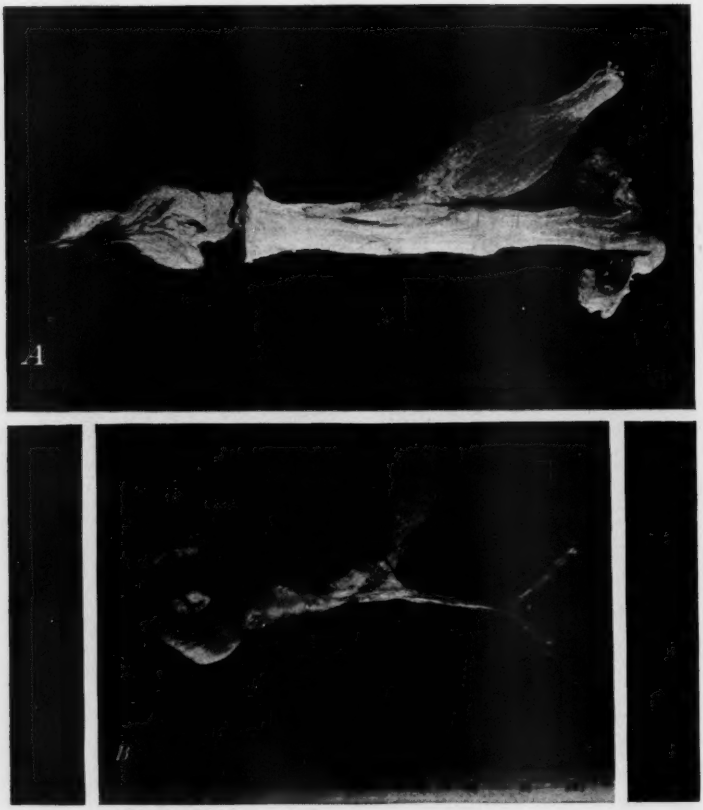
A, Section through a rear quarter of the udder of freemartin No. 806 at 8 months 22 days of age; *B*, section through rear quarter of the udder of normal heifer No. 68 U. S. at 9 months 2 days of age.



A, Section through a rear quarter of the udder of normal heifer No. 75 U. S. at 6 months 1 day of age; *B*, section through rear quarter of the udder of normal heifer No. 1259 at 6 months of age.

A, Section through a rear quarter of the udder of freemartin No. 1427 at 6 months 1 day of age; *B*, section through a rear quarter of the udder of freemartin No. 1229 at 3 months of age; *C*, section through a rear quarter of the udder of normal heifer No. 686 at 3 months 19 days of age.

Internal genitalia of A–70. This freemartin had reproductive organs of intermediate development, but no cervix.



A, Internal genital tract of No. 1205, twinborn with a bull calf but apparently a normal heifer; *B*, the rudimentary genital tract of freemartin No. 1485 at approximately the same age.

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